Fisheries and Oceans Canada | Pêches et Océans Canada
Science | Sciences

CSAS | **SCCS**

Canadian Science Advisory Secretariat | **Secrétariat canadien de consultation scientifique**

Research Document 2008/007 | **Document de recherche 2008/007**

Recovery potential assessment for lake sturgeon (*Acipenser fulvescens*) in Canadian designatable units

Évaluation du potentiel de rétablissement de l'esturgeon jaune (*Acipenser fulvescens*) dans les unités désignables canadiennes

Luis A. Vélez-Espino and Marten A. Koops

Great Lakes Laboratory for Fisheries and Aquatic Sciences
Fisheries and Oceans Canada
867 Lakeshore Road
Burlington, ON, L7R 4A6

* This series documents the scientific basis for the evaluation of fisheries resources in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

Research documents are produced in the official language in which they are provided to the Secretariat.

This document is available on the Internet at:

* La présente série documente les bases scientifiques des évaluations des ressources halieutiques du Canada. Elle traite des problèmes courants selon les échéanciers dictés. Les documents qu'elle contient ne doivent pas être considérés comme des énoncés définitifs sur les sujets traités, mais plutôt comme des rapports d'étape sur les études en cours.

Les documents de recherche sont publiés dans la langue officielle utilisée dans le manuscrit envoyé au Secrétariat.

Ce document est disponible sur l'Internet à:

http://www.dfo-mpo.gc.ca/csas/

ISSN 1499-3848 (Printed / Imprimé)
© Her Majesty the Queen in Right of Canada, 2008
© Sa Majesté la Reine du Chef du Canada, 2008

Canada

ABSTRACT

Following a recommendation from the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), recovery potential assessment (RPA) is required to inform the listing decision under the *Species at Risk Act* (SARA). COSEWIC's assessment divided the lake sturgeon (*Acipenser fulvescens*) geographic distribution into eight designatable units (DUs), recommending conservation statuses of Special Concern (DU6 and DU7), Threatened (DU8), and Endangered (DU1 to DU5). Here we present modelling in support of an RPA using stage-structured matrix models to quantitatively assess allowable harm, recovery efforts, probabilities of recovery and recovery timeframes. From this assessment, we conclude that lake sturgeon populations are most sensitive to harm on adult survival. However, maximum proportional increases in population growth rates can be achieved by focusing recovery efforts on YOY and juvenile survival. Finally, based on a recovery target of 1188 spawning females per year and assuming that current abundances are 10% of this target, the time to 95% probability of recovery range from 20 years to over 100 years (1-3 generations), depending on the recovery actions implemented.

RÉSUMÉ

En vertu d'une recommandation du Comité sur la situation des espèces en péril au Canada (COSEPAC), une évaluation du potentiel de rétablissement (EPR) est requise pour éclairer les décisions concernant l'inscription de l'espèce en vertu de la *Loi sur les espèces en péril* (LEP). L'évaluation du COSEPAC divise l'aire de répartition géographique de l'esturgeon jaune (*Acipenser fulvescens*) en huit unités désignables (UD) et recommande, aux fins de la conservation, que les UD 6 et 7 soit considérées comme préoccupantes, que l'UD8 soit considérée comme menacée et que les UD 1 à 5 soient considérées comme en voie de disparition. Dans le présent document, nous présentons une modélisation effectuée à l'appui d'une EPR à l'aide de modèles matriciels structurés en fonction du stade de développement pour évaluer de façon quantitative les dommages admissibles, les efforts de rétablissement, les probabilités de rétablissement et les échéanciers du rétablissement. Selon cette évaluation, nous concluons que la vulnérabilité des populations d'esturgeons jaunes est plus importante lorsque des dommages mettent la survie des adultes en péril. Cependant, des augmentations proportionnelles maximales des taux de croissance démographique peuvent être obtenues en concentrant les efforts de rétablissement sur la survie des jeunes de l'année et des juvéniles. Ainsi, avec une cible de rétablissement de 1188 femelles reproductrices par année et selon l'hypothèse que l'abondance actuelle soit de 10 % de cette cible, le délai de rétablissement, selon une probabilité de 95 %, varie de 20 à plus de 100 ans (de 1 à 3 générations), selon les mesures de rétablissement mises en œuvre.

INTRODUCTION

Lake sturgeon (*Acipenser fulvescens*) is one of five sturgeon species found in Canadian waters and the only species that completes its life cycle exclusively in freshwater (Scott and Crossman 1998). Based on the freshwater ecological areas used by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) and published genetic studies, eight biogeographically distinct designatable units (DUs) were identified for lake sturgeon (COSEWIC 2006; Figure 1). Lake sturgeon has been recommended by COSEWIC (2006) for conservation statuses of Special Concern (DU6 and DU7), Threatened (DU8), and Endangered (DU1 to DU5).

A recovery potential assessment (RPA) consists of three phases: determination of species/population/management unit status, assessment of the scope for human-induced harm (allowable harm), and the identification of mitigation strategies (DFO 2005a; DFO 2005b). Once a species is listed as endangered or threatened, SARA restricts harm from human activities under the conditions set out in section 73(3):

(a) all reasonable alternatives to the activity that would reduce the impact on the species have been considered and the best solution has been adopted;

(b) all feasible measures will be taken to minimize the impact of the activity on the species or its critical habitat or the residences of its individuals; and

(c) the activity will not jeopardize the survival or recovery of the species.

Modelling in support of an RPA provides scientific advice in support of paragraph 73(3)(c) about the levels of harm a species (or population) could sustain without compromising the above conditions.

A demographic approach to assessing recovery potential in aquatic species at risk with minimal data and based on life-history information was developed by Vélez-Espino and Koops (2007*a*, *b*) to provide a quantitative approach to the RPA components applied to freshwater species at risk. Briefly, the approach relies on demographic modelling widely applied in conservation biology (e.g., Crouse et al. 1987; Cortés 2002; Wilson 2003), resource management (e.g., Getz and Haight 1989; Hayes 2000) and pest control (Rockwell et al. 1997; Shea and Kelly 1998; Neubert and Caswell 2000), in which harm is defined as a negative perturbation that can target one or more vital rates and life stages simultaneously. This quantitative assessment of allowable harm uses perturbation analysis, a demographic prospective technique that depends on the construction of projection matrices from which population growth rate (λ) can be calculated and the relative sensitivity of each vital rate (i.e., elasticities) can be used to project the effects of management interventions (Caswell 2000). Within this framework, allowable harm is a function of (*i*) the vital rate(s) impacted by human action(s), (*ii*) the sensitivity of impacted vital rate(s), (*iii*) the population growth rate before harm, and (*iv*) the minimum population growth rate that will not jeopardize the survival and future recovery of the population. Population growth rate will be susceptible not only to direct human-induced mortality but also to indirect suppression of reproduction and growth by human actions. Additionally, this approach has minimal data requirements while using all available data, can link population dynamics with habitat-based information, is flexible enough to assess complex life histories, and follows a precautionary approach.

Any RPA requires the identification of recovery targets, imeframes for recovery, and specification of the uncertainty of outcomes associated with management actions (DFO 2005a; DFO2005b). DFO's (2005c) framework for developing science advice on recovery targets for aquatic species at risk identified direct estimates of total popul tion size and total geographic range as the preferred currencies for specifying recovery targets and focusing recovery efforts (i.e., the strategic means by which recovery targets are achieved). From a demographic perspective, recovery efforts can be defined as the minimum increases in vital rates (i.e., survival, reproduction, growth) necessary to stabilize population growth rates or generate a growing population. Thus, recovery effort is really an inverse expression of allowable harm for a specific vital rate (Vélez-Espino and Koops *2007b*).

We apply perturbation analyses of a stage-structured matrix population model and population viability analysis in support of a recovery potential assessment for lake sturgeon. Our goals are to (*i*) estimate maximum allowable harm and minimum recovery efforts for individual vital rates, (*ii*) contrast alternative models in support of a precautionary approach, and (iii) generate long-term projections of recovery timeframes under alternative management scenarios.

METHODS

Our analysis entailed 5 steps. First, life history data were compiled from the literature and management agencies to determine age-specific vital rates (such as survival and fertility) for each DU. Second, these vital rates were used to build individual stage-structured projection matrices for each DU. Third, deterministic and stochastic matrix perturbation analyses were conducted following the approach described by Vélez-Espino and Koops (2007*a, b*) to determine allowable harm and recovery efforts. Fourth, a precautionary approach was implemented to provide management recommendations pertinent to each DU. Finally, information on recovery targets and recovery efforts were combined in a stochastic process to compute probabilities of recovery and recovery timeframes.

Somatic growth and fecundity

Lake sturgeon life history data were compiled from various sources (see Table 1). Length and weight relationships for lake sturgeon from Lake Nipigon (DU8; Scott and Crossman 1973), and the Ottawa River (DU8; Haxton 2002), were contrasted with a recent assessment which produced the relationship log_{10} Weight (kg) = -8.323 + 3.033 log_{10} Total Length (mm) (R^2 = 0.88; p = 0.0001; n = 271) for lake sturgeon from Rainy Lake (Adams 2004), located at the northern Minnesota-Ontario border (DU6). Data from Lake Nipigon and the Ottawa River were well represented by this predictive regression (Figure 2*a*), suggesting that the lake sturgeon length-weight relationship is preserved throughout its range. Although in present times large sturgeon are usually less than 40 kg (Scott and Crossman 1998), the relationship between historical maximum length (3 m) and weight (180 kg) reported in Stewart and Watkinson (2004) is also well represented by Adams' (2004) length-weight equation.

Direct determination of growth patterns for individual populations, and even at the DU level, is currently unachievable given the paucity of available data. Fortin et al. (1996) studied length and body condition of lake sturgeon throughout most of the species

distribution and found that a multivariate model incorporating latitude (LAT) and longitude (LON) explained a high proportion (67%) of the variation in mean total length for the age interval 23-27 ($TL_{23\text{-}27}$):

1) $$TL_{23\text{-}27} = 2569.6 - 49.1LAT + 11.4LON$$

We tested the accuracy of equation 1 to represent total length-at-age of the Lake Nipigon and Rainy Lake populations. Adams (2004) generated the Rainy Lake population growth model $TL_t(\text{cm}) = 140.4\ (1\text{-}e^{-0.11\ (t0\ -\ 0.56)})$. Using the Lake Nipigon data we generated the growth model $TL_t\ (\text{cm}) = 229.8\ (1\text{-}e^{-0.11\ (t0\ +\ 2.8)})$. We used latitudes and longitudes at the centroid of both aquatic systems (Mapping Services Branch of Natural Resources Canada; http://geonames.nrcan.gc.ca/) with age 25 as the dependent variable, and found that TL_{25} in the Rainy Lake and Lake Nipigon populations was predicted effectively by Fortin et al.'s (1996) equation (Figure 2b). Supported by these results, we developed individual growth models for each lake sturgeon DU (Figures 3*a*, 4*a*) by computing the von Bertalanffy growth coefficient (k) as a function of TL_{25}

2) $$k = \frac{\ln\left(1 - \frac{TL_{25}}{L_\infty}\right)}{-25}$$

assuming that t_0 in the growth model is zero, and using an asymptotic length (L_∞) that varies with latitude (Table 2). Latitudes and longitudes at the center of the main aquatic systems within DUs were averaged to obtain a singular value of TL_{25} for each DU.

Power and McKinley (1997) provide evidence of a latitudinal gradient in lake sturgeon growth rates. Across 17 lake sturgeon populations (data from Power and McKinley 1997, Adams 2004), a significant proportion of the variation in asymptotic length was explained by latitude using a linear regression (L_∞ = -3.47 LAT + 322.88; R^2 = 0.3, p = 0.02; n = 17). We applied this regression to the average central latitude of aquatic systems within DUs to determine asymptotic lengths. One potential limitation of representing growth this way is the use of a unique geographic centroid for an entire DU. While appropriate for DUs where lake sturgeon occupy few well defined systems, important variation may be lost by averaging geographic coordinates across distant locations within a large DU. Thus, dividing large DUs or those with distant discrete populations, such as DU8 (Great Lakes-Western St. Lawrence), into smaller sub-units may be advisable. Given its threatened conservation status and the existence of localized commercial harvest, DU8 was divided in three sub-units: Lake Erie-Lake Huron ($DU8_A$), North Lake Superior ($DU8_B$), and St. Lawrence ($DU8_C$). Note that the importance of this will diminish if observed variability in growth and fecundity within DUs is higher than the modelled variability between DUs when it might be more appropriate to build a generic lake sturgeon stochastic model incorporating variability in growth and fecundity (see below).

Weight-at-age for each DU was computed by combining data on length-at-age generated by the DU-customized von Bertalanffy model and length-weight relationship (Figures 3*b*, 4*b*). Lastly, weight-at-age data were combined with a mean relative fecundity of 12 000 eggs per kilogram of body weight (USFWS 2006) to determine number of eggs at age (m_i), starting from a minimum age of maturity of 14 years (USFWS 2006). Considering the lack of evidence for reproductive senescence (Figures 3*c*, 3*c*), the number of eggs continues to increase with age (Stewart and Watkinson 2004). The relative fecundity value of 12 000

eggs per kilogram is consistent with observed data presented by Scott and Crossman (1973; Figure 2*c*). Age-specific fertility (f_i), defined as the annual number of females produced per female, was computed as the product of the number of eggs (m_i), an even sex ratio (50% of eggs produce females; Fortin et al. 1993), and the inverse of the average spawning periodicity (5 years; Wallace 1991, Winemiller and Rose 1992).

Vital rates

The life cycle of lake sturgeon was represented with annual projection intervals and a stage-structured projection matrix with five life stages: young-of-the-year (YOY), early juvenile, late juvenile, early adult, and late adult (Figure 5). In our model, the juvenile stage is the period from the end of the first year to the mean age at first maturity (24 years; USFWS 2006), with the early and late juvenile stages being the first and second half of this period, respectively. The early and late adult stages refer to the first and second half of the adult period, respectively, which covers the period from mean age at first maturity to maximum reproductive age where total length is 95% of asymptotic length. This was considered necessary to account for differences in growth patterns influencing stage duration; maximum age would be over-estimated if based solely on asymptotic length. Consequently, the duration of both adult stages differed among DUs. Subdividing juveniles and adults into early and late stages reduces information loss from averaging vital rates with high variances in species with long juvenile or adult periods (see Crouse et al. 1987). The elements of a stage structured matrix generally include the fecundity coefficient of stage class j (F_j), the probability of surviving stage j and remaining in stage j (P_j), and the transition probability of surviving one stage and moving to the next (G_j). A stage-structured model requires σ_j as the annual survival probability of an individual in stage j, and γ_j as the probability of moving from j to j+1 given σ_j. Then, the parameters P_j and G_j are defined as $\sigma_j (1- \gamma_j)$ and $\sigma_j \gamma_j$, respectively. The term γ_j is calculated from a geometric distribution of $1/T_j$ where T_j is the duration of stage j.

We used a separate post-breeding projection matrix (see Caswell 2001) for each DU. In this model, fecundity coefficients (F) depend on adult survival through the previous year as well as the stage-specific fertility f_j such that:

3) $$F_j = f_j P_j + f_{j+1} G_j$$

where f_j is the average fertility across all age classes within a stage and P_j and G_j are calculated from the average age-specific survival rate σ_i (see below) within a given stage (σ_j). According to equation 3, juveniles moving into the young-adult stage the following year will contribute to the reproductive output because a post-breeding variant assumes the census is taken after spawning, (Crowder et al. 1994), hence the additional element $f_4 G_3$ (Figure 5c). Following Vélez-Espino et al. (2006), annual survival at age i for juvenile lake sturgeon one-year old and older was estimated as:

4) $$\sigma_i = \sigma_A^{i/\alpha}$$

were α is the mean age of first maturity and σ_A is the annual survival of adult fish. The term σ_A was estimated from the life history invariant M/k = 1.65 (Charnov 1993, Jensen 1996), where M is the mortality rate. The M/k invariant produces adult survival values (0.86-0.93) similar to those reported for adult lake sturgeon elsewhere (Wallace 1991, MacDonnell

1998, Adams 2004, Vélez-Espino et al. 2006). The M/k invariant was also found to perform relatively well among 5 Great Lakes fishes (Koops and Chu 2007).

Once all vital rates for the eight DUs were computed, YOY survival was calculated for each DU by solving for the geometric mean population growth rate Λ (see below) without altering any other matrix element. This involved an iterative process using elasticities (see below) for a first iteration through direct perturbation of the projection matrices (Vélez-Espino et al. 2006).

Perturbation analysis

For a thorough description of the assessment of allowable harm and recovery efforts within a demographic framework refer to Vélez-Espino and Koops (2007*a*, *b*). Briefly, annual population growth rate (λ),represented by the largest eigenvalue of a projection matrix, integrates impacts on the survival and recovery of a population. Using this metric of population growth, a population at equilibrium will have a $\lambda = 1$, a growing population will have a $\lambda > 1$, and a population exhibiting annual abundance decreases will have a $\lambda < 1$. Setting equilibrium as the minimum acceptable population growth rate (i.e., $\lambda = 1$), allowable harm (τ_v) and maximum allowable harm ($\tau_{v,max}$) can be analytically calculated as:

$$\tau_v \leq (1/\varepsilon_v)\frac{1 - \Lambda}{\Lambda} \qquad 5)$$

$$\tau_{v,max} = (1/\varepsilon_v)\frac{1 - \Lambda}{\Lambda}$$

Similarly, recovery effort (ψ_v) and minimum recovery effort ($\psi_{v,min}$) have the form

$$\psi_v \geq (1/\varepsilon_v)\frac{\lambda_{Target} - \Lambda}{\Lambda} \qquad 6)$$

$$\psi_{v,min} = (1/\varepsilon_v)\frac{\lambda_{Target} - \Lambda}{\Lambda}$$

where ε_v is the elasticity (a measure of the sensitivity of population growth rate) of vital rate v, λ_{Target} is the target population growth rate to achieve recovery within a desired recovery timeframe, and Λ represents the geometric mean population growth rate before harm or mitigation actions. The term Λ was calculated from (*i*) the population growth rate determined by COSEWIC's criterion "A" for the status assessment of species based on observed or inferred rates of population decline ($\lambda_{designation}$), (*ii*) the maximum population growth at low densities determined from Randall and Minns' (2000) allometry between production per unit biomass and weight at maturity for freshwater fishes ($\lambda_{max} = e^{2.64W^{-0.35}}$; W = weight at first maturity (g)), and (*iii*) equilibrium ($\lambda_{equilibrium}$) as an important dynamic attractor (Turchin 1995).

Under COSEWIC's criterion A, a species is assessed as endangered if evidence indicates a 70% decline over 10 years or three generations (3ς, i.e., $\lambda = 0.3^{1/10}$ or $\lambda = 0.3^{1/3\varsigma}$), whichever indicates a greater decline, and as threatened if evidence indicates a 50%

decline over the last 10 years or three generations (i.e., $\lambda = 0.5^{1/10}$ or $\lambda = 0.5^{1/3_5}$), whichever indicates a greater decline. There is no equivalent measure of $\lambda_{designation}$ for special concern populations because according to COSEWIC criteria a species can be treated as of special concern when the decline is not sufficient to qualify as threatened but the species is considered likely to become threatened if potential causes of decline are not reversed. Thus, we used $\lambda_{designation} = 1$ to represent these conditions of special concern. In addition, given that life-table analysis indicates DU generation times ranging from 29 to 40 years, $\lambda_{designation}$ was 0.89 for DUs 1 to 5 and 0.93 for DU 8. Under these conditions, Λ in lake sturgeon DUs ranged from 0.99 to 1.04 (Table 3). Following Vélez-Espino and Koops (2007*a, b*), allowable harm analysis was conducted exclusively in populations with $\Lambda > 1$. Populations with $\Lambda < 1$ are candidates for the analysis of recovery efforts. Thus, allowable harm was assessed in DUs 1, 3, 6, 7, and 8; recovery effort was assessed in the remaining DUs. Given that recovery targets or recovery timeframes for lake sturgeon have not been defined, recovery efforts were calculated with $\lambda_{Target} = \Lambda^{-1}$ for DUs with a geometric population growth rate less than 1 (Table 3). The rationale was to generate recovery efforts mirroring population trends (i.e., reversing population trends at the same rate) but any other λ_{Target} can be implemented on the basis of desired recovery timeframes and feasible demographic performance of the population in question. For instance, it is well known that a long-lived, large, slow-growing, late maturing, intermittent spawning species, such as lake sturgeon, cannot exhibit maximum population growth rates as high as those exhibited by short-lived, small, fast-growing, early maturing, annually spawning species (Pianka 1970, Reznick et al. 2002).

For projection matrices, sensitivity of population growth rate to perturbations in the vital rates is calculated by the elasticities ($\varepsilon_{kl} = \delta \log \lambda / \delta \log m_{kl}$). For instance, a 20% decrease in the adult survival rate of a population with an adult survival elasticity of 0.1 will produce a 2% decrease in the population growth rate (i.e., 100 x 0.2 x 0.1; see also De Kroon et al. 1986, Brault and Caswell 1993, Hitchcock and Grato-Trevor 1997). However, the vital rate with the greatest elasticity will not always be the management target for both allowable harm and recovery effort. More specifically, recommendations on recovery efforts, which depend on the ability to increase population growth rates from improvements in individual vital rates, will depend not only on the elasticities of survival or fecundity rates but also on how the room for improvement in each vital rate (Morris and Doak 2002). This should be particularly important for lake sturgeon, in which adult survival is close to 1. Consequently, we estimated the maximum proportional change in λ due to changes in a vital rate v_j as:

7) $$\Delta\lambda/\lambda = \varepsilon_{vj}\left(v_{j,max} - v_j\right)\Big/ v_j$$

where v_j is the mean value of the vital rate and $v_{j,max}$ is the maximum value determined for that vital rate. Maximum vital rate values were estimated separately for each DU. Maximum YOY survival ($\sigma_{1,max}$) was calculated from 100% increments in the original value of this vital rate. Maximum survival rates for early juvenile ($\sigma_{2,max}$) and late juvenile ($\sigma_{3,max}$) stages were represented by the survival rate of the oldest age class in each stage. Given the high survival of adult lake sturgeon, maximum survival rate for early ($\sigma_{4,max}$) and late ($\sigma_{5,max}$) adult was fixed at 1. Lastly, maximum fertility rates of early ($f_{4,max}$) and old ($f_{5,max}$) adult were represented by the fertility rate of the oldest age class in each stage. The term $\Delta\lambda/\lambda$ was estimated by computer simulation incorporating uncertainty in vital rates (see stochastic approach below).

Alternative models

Three alternative models were used in the recovery potential assessment: deterministic for individual DUs, stochastic for individual DUs, and stochastic-generic across all DUs. The results of these models were contrasted in light of two processes: (*i*) the application of a precautionary approach, and (*ii*) the principle of parsimony, which, in the absence of evidence to the contrary, favours the simplest approach possible.

Deterministic models

The deterministic approach uses analytical solutions that incorporate elasticity values of mean vital rate estimates. However, these analytical solutions are expected to be robust for perturbations up to 30% and occasionally up to 50% (Caswell 2001). Non-linearities, often exhibited between vital rates and population growth (see Mills et al. 1999; de Kroon et al. 2000), reduce the accuracy of projections using elasticities as perturbations get larger. Following Vélez-Espino and Koops (2007*a*), we assessed allowable harm and recovery efforts by directly perturbing the projection matrices. Direct perturbations involve altering the vital rate in question while keeping all other matrix elements constant until the largest eigenvalue of the matrix is 1 (for allowable harm) or λ_{Target} (for recovery effort). The first iteration used results from the analytical solution (equations 5 and 6).

Stochastic models

The stochastic approach incorporates observed variation in vital rates within each DUs (see Appendix) For this model, we used simulations to generate 1000 random matrices. The beta distribution, with a mean equal to σ_j and variance generated by all age classes within each stage, was used to simulate variation in juvenile survival. This distribution is appropriate for binary events, such as survival, and produces random variables confined to the interval 0 to 1. Given the lack of multiple values for YOY and adult survival from which to estimate variance, values for these vital rates were drawn from uniform distributions. The distribution for YOY survival used $\sigma_{1,max}$ and $0.5\sigma_1$ as upper and lower distribution limits, respectively. The distribution for adult survival used $\sigma_{j,max}$ and $0.95\sigma_j$ as upper and lower distribution limits, respectively. The lognormal distribution was used to simulate fertility values with a mean equal to f_j and variance generated by all age classes within each adult stage. This distribution produces only positive random variables bounded by zero and infinity, and is particularly appropriate for organisms with numerous offspring (e.g., Mertz and Myers 1996). Population growth rate and elasticities of vital rates were calculated for each matrix; a parametric bootstrap was used to estimate mean stochastic elasticities and their 95% confidence intervals. In addition, maximum proportional increases in population growth rate ($\Delta\lambda/\lambda$) were computed from the mean values of stochastic elasticities.

Stochastic-generic model

The indirect way of estimating growth and fecundity differences between DUs opens the possibility of artificial contrasts. To assess the importance of this source of uncertainty, we incorporate vital rate variation among DUs into a single generic model. A recovery potential assessment of this sort would be consistent with the principle of parsimony (i.e., the simplest inclusive approach) while potentially generating precautionary estimates of

allowable harm and recovery efforts that could assist management recommendations. We implemented a stochastic-generic model using the same methodology described for the stochastic model but with stochastic distribution parameters computed from the pool of data across DUs. Given the variation in transition probabilities of adult stages between DUs, the generic model used the average values of early and late adult transition probabilities. Allowable harm was assessed using the arithmetic mean of all positive Λ's whereas recovery efforts were assessed using the arithmetic mean of all Λ's less than 1 and the inverse of this number as λ_{Target}. Maximum proportional increases in population growth rate ($\Delta\lambda/\lambda$), computed from the mean stochastic elasticities, used the highest values among all DU maxima as $v_{j,max}$.

Precautionary approach

Maximum allowable harm ($\tau_{v,max}$) and minimum recovery effort ($\psi_{v,min}$) for vital rates were summarized in comprehensive tables as suggested by Vélez-Espino and Koops (2007*a, b*) where deterministic results from analytical solutions (elasticities) and direct perturbations of projection matrices were contrasted with those generated from the stochastic model for individual DUs, and the stochastic-generic model. Following a precautionary approach, lower bounds of the confidence intervals generated by both stochastic models were used (see Richards and Maguire 1998) for the analysis of allowable harm, and upper confidence interval bounds for the analysis of recovery efforts (Vélez-Espino and Koops 2007*a, b*). Allowable harm recommendations were based on the least negative value of allowable harm among the four outputs for each vital rate ($\tau_{v,precautionary}$). The critical or most sensitive vital rate was identified as the one with the least scope for harm. Recovery effort recommendations were based on two criteria: (*i*) the highest value among the four outputs ($\psi_{v,precautionary}$) and (*ii*) the feasibility index (δ_j): greatest positive difference between the maximum proportional increase in a vital rate, $(v_{j,max} - v_j) / v_j$, and the precautionary minimum recovery effort:

8) $$\delta_j = \frac{v_{j,\max} - v_j}{v_j} - \psi_{v,precautionary}$$

Vital rates recommended as preferred targets for recovery efforts were those with the lowest precautionary recovery effort ($\psi_{v,precautionary}$) and the highest feasibility for improvement (δ_j).

Recovery targets

Among the population-based approaches (e.g., evolutionary potential, demographic sustainability, ecological function, social dynamics, historical baseline, maximum, or status quo) available to set population targets, seeking demographic sustainability is considered the most conservative and quantitatively feasible (Sanderson 2006). Achieving demographic sustainability is suitable for setting recovery targets not only because demography is more tractable than other aspects of animal ecology such as genetics, behaviour, or ecological function, but demographic data are amenable to the family of population modelling tools referred to as population viability analysis (PVA: Beissinger and McCullough 2002, Sanderson 2006).

With demographic sustainability (i.e., population is self-sustaining over the long term) as the appropriate criterion to set recovery targets, we used Reed et al.'s (2003) allometry between maximum population growth rate and minimum viable population size (*MVP*; Sheffer 1981). The recovery target was set as the minimum population size required for a 99% probability of persistence over 40 generations. Using this predictive equation ($\ln MVP = 9.5 - 1.8 \ln R_0$; $R^2 = 0.8$; $p < 0.01$; R_0 = maximum population growth rate per generation), *MVP* was computed separately for each lake sturgeon DU.

Reproductive effort was included in our definition of recovery targets to account for spawning periodicity (ξ) which ranges from 3 to 7 years in female lake sturgeon (Wallace 1991). However, within this interval the proportion of adult females exhibiting each reproductive periodicity in a given year is uncertain. Parsimoniously, assuming that the five patterns of spawning periodicity (3, 4, 5, 6, and 7 years) are equally represented, recovery targets for each DU were computed as a weighted mean of the annual number of spawning females (*ASF*):

9) $$ASF = \sum_{\xi=3}^{7} \frac{1}{\xi} \frac{1}{n} MVP_{Females}$$

where n is the number of potential scenarios for spawning periodicity ($n = 5$) and $MVP_{Females}$ is the female portion of the minimum viable adult population as determined by the sex ratio (assumed even). This produced an average recovery target of 1188 spawning females per year with 95% confidence limits of 1160-1216.

Recovery efforts were combined with recovery targets to project recovery timeframes as a stochastic process. We used a stochastic approach to calculate recovery timeframes. Considering recovery as a stochastic process, time to recovery is uncertain and the probability of reaching the recovery target becomes the response parameter. Therefore we calculate recovery timeframes as the time to attain a 95% probability of reaching the recovery target, departing from an initial population vector (*IPV*) representing 1-10% of the recovery target (*ASF*). The number of females distributed among reproductive stages and the abundances of juvenile stages were determined from the stable stage distribution, which is represented by the dominant right eigenvector (w) of the original projection matrix ($\mathbf{A}w = \lambda w$) and indicates the expected proportion of the population in age class i should vital rates remain relatively constant (de Kroon et al. 1986). Initial population vectors were calculated from the average stable age distribution calculated from 10 transition matrices corresponding to all lake sturgeon DUs. We initiated simulations at 1-10% of the recovery target because (*i*) current lake sturgeon abundance estimates do not exist for most aquatic systems, (*ii*) with few exceptions (e.g., Lake of the Woods and Rainy River; Stewig 2005), recent studies reporting abundance estimates of lake sturgeon show populations considerably lower (<10%) than the recovery target for demographic sustainability (e.g., Baker and Borgeson 1999, Peterson et al. 2001, Earle 2002, Thomas and Hass 2002), and (*iii*) there is evidence that lake sturgeon populations throughout the Great Lakes and surrounding waterbodies have declined to less than 1% of their historic abundances (Hay-Chmielewski and Whelan 1997). The probability of recovery was computed with Monte Carlo simulations randomly selecting projection matrices representing potential population states. 5000 realizations of population size were used to generate a cumulative distribution function (CDF) for the time to reach the recovery target. Probability of recovery at time t was computed as the proportion of realizations of population size reaching or exceeding the recovery target at time t.

We explore the sensitivity of stochastic projections to spawning periodicity by accounting for extreme scenarios caused by environmental influences. Recovery timeframes were computed from two separate sets of simulations incorporating altered projection matrices. The first simulation set randomly selected altered projection matrices characterized by fertilities estimated with an average spawning periodicity of three years. The second simulation set used an average spawning periodicity of seven years.

RESULTS

Deterministic models

Elasticities computed from mean matrices clearly point early adult survival (σ_4) as the vital rate most sensitive to perturbations in all lake sturgeon DUs (Figure 6*a*), although important variability was present among DUs (elasticity range: 0.33-0.50). Population growth rates of lake sturgeon DUs exhibited low-medium sensitivity to perturbation in all other survival rates and even lower sensitivity to perturbations in fecundity rates of both adult stages (elasticity range: 0.02-0.07). This elasticity pattern was reflected in the estimates of maximum allowable reduction in early adult survival of only 1.5-9.2%, followed late juvenile (3.0-18.8%) and late adult (4.6-33.3%) survival. YOY and early juvenile survival showed intermediate values of maximum allowable harm (8.3-52.0% in YOY; 6.2-38.8% in early juveniles). Maximum allowable reduction of fertility rates was high (12.8-73.7%) in both early and late (23.5-100%) adults. Results from direct perturbations of the projection matrices closely matched analytical results (Table 4).

Minimum recovery effort analysis indicated that to reach target population growth rates (λ_{Target}) in DUs 2, 4, and 5, early adult survival must increase 1.4-4.3%, late adult survival by 4.0-12.9%, and late juvenile survival by 2.4-4.8%. Larger increases are needed in YOY (6.9-13.5%) and early juvenile (5.1-10.0%) survival. Minimum recovery efforts estimated for early and late adult fertility ranged up to 21.4% and 36.6%, respectively. Again, direct perturbation results closely matched those obtained analytically (Table 5).

Considering the feasibility to improve population growth rates through any given vital rate, maximum proportional increase in population growth rate ($\Delta\lambda/\lambda$) of all DUs (Figure 7*a*) was highest for YOY (6.4-11.2%) and early juvenile (6.4-10.9%) survival, medium for late juvenile (5.0-7.8%) and early adult (3.7-5.4%) survival, low for late adult survival (1.2-1.8%) and early adult fertility (0.6-1.9%), and negligible for late adult fertility (0.2-0.3%). Thus, although population growth is highly sensitive (high elasticity) to early adult survival, the potential to increase this vital rate limits improvements to population growth rates. In spite of the low elasticities of YOY and early juvenile survival, their high potential for improvement increases their effects on population growth. This will impact management recommendations concerning recovery efforts since biological or ecological limits constrain vital rate increments.

Stochastic models

Stochastically computed elasticities produced a pattern similar to the deterministic approach (Figure 6*b*). Wide confidence intervals relative to the means characterized the elasticities of all vital rates, particularly confidence intervals of late adult survival (σ_5) elasticities whose upper bounds (range: 0.33-0.54) closely approached the height of the

upper bounds associated with early adult survival (σ_4; range: 0.51-0.70). This elasticity pattern translated into lower estimates of maximum allowable harm compared to the deterministic estimates, but the ranking of susceptibility to harm was conserved among vital rates and across DUs.

Relative differences between deterministic and stochastic estimates were greater for minimum recovery efforts than for maximum allowable harm (Table 5). Increasing early adult survival by up to 6% is expected to reverse declining trends and achieve target population growth rates in DUs 2, 4, and 5. Minimum recovery efforts for other vital rates must be substantially higher, ranging up to 18% in late juvenile survival, 29% in late adult survival, 36% in early juvenile survival, 40% in YOY survival, 62% in late adult fertility, and over 100% in early adult fertility.

Stochastic computation of the maximum proportional increases in population growth rate ($\Delta\lambda/\lambda$)generated similar patterns to deterministic estimates (Figure 7). Nevertheless, in this case the maximization of YOY survival did not produce values of $\Delta\lambda/\lambda$ (range: 5.3-8.8%) as high as those of early juvenile survival (range: 6.4-10.4%), as was the case with the deterministic approach, and the rank of $\Delta\lambda/\lambda$ for late juvenile survival increased (range: 6.2-8.6%) relative to that achieved in the deterministic approach. Maximum proportional increases in λ was 4.1-5.9% for early adult survival, 1.7-2.4% for late adult survival, 0.6-1.9% for early adult fertility, and 0.17-0.25% for late adult fertility.

Stochastic-generic model

Stochastic elasticities computed from the generic model were representative of those computed by the stochastic model of individual DUs. Confidence intervals were no wider than those produced by the DU-specific modelling. But, the generic model generated lower estimates of maximum allowable harm in some vital rates of DUs 6, 7, and 8_A (see Table 4). Maximum allowable harm estimated from the generic model ranged from 2.9% in early juvenile survival to 49.3% in late adult fertility. Further, minimum recovery efforts estimated by the generic model preserved the rank order produced by the stochastic models of individual DUs and generated values ranging from 4.3% in early adult survival to 59.4% in late adult fertility. The generic model produced higher estimates of minimum recovery efforts for all vital rates in DU4, most vital rates in DU2, and late adult survival in DU5 (Table 5).

Precautionary estimates

The deterministic approach did not produce precautionary values of maximum allowable harm for any DUs whereas the stochastic model for individual DUs produced precautionary values of maximum allowable harm for all vital rates in DUs 1, 3, and 8, with the exception of late adult fertility in $DU8_A$. The stochastic-generic model produced precautionary values for all remaining DU vital rates, including all vital rates in special concern DUs 6 and 7. Early adult survival was identified as the vital rate most vulnerable to harm in all DUs, closely followed by late adult survival. Maximum allowable harm in early adult survival should not exceed 3% in DUs 1, 3, 6, 7, 8_A, 8_B, and 8_C if their survival and recovery is not to be risked. At the other extreme, late adult fertility exhibited the greatest resilience to harm, with a maximum allowable harm ranging up to 49%. Further, DU1 and $DU8_C$ exhibited the "most precautionary" values of allowable harm.

The deterministic model did not generate precautionary minimum recovery efforts for any DUs, whereas the stochastic models produced precautionary values of minimum recovery efforts for early and late adult survival in DU2, and all vital rates, excepting late adult survival, in DU5. The stochastic-generic model produced precautionary values for all vital rates in DU4 and for late adult survival in DU5. Both, low recovery efforts and positive feasibility indices (δ_j) in DUs 2, 4, and 5 suggest that targeting early adult survival for mitigation activities is recommended. In addition, given that the feasibility index for YOY and early juvenile survival are higher than any other vital rate in these DUs, YOY and juvenile survival is also recommended for mitigation activities. Further, DU5 exhibited the "most precautionary" values of minimum recovery efforts for all vital rates except adult survival whose most precautionary values were exhibited in DU2.

Recovery timeframes

A variety of management scenarios targeting different combinations of vital rates were simulated with recovery strategies derived from habitat rehabilitation, stocking, fishing regulations, and improved fish passage at barriers. The proactive nature of the recovery strategies increase from strategy 1 to 5 with each strategy adding to the actions of the previous strategy. Strategy 1 maximizes survival of early adults (e.g., by total closure of the fishery on early adults), as the vital rate with the highest contribution to population growth rates. Late juvenile survival rate makes the second largest contribution to population growth and its maximum proportional increase was less than 26%. Strategy 2 adds a 10% increase in the survival of late juveniles (e.g., by increasing minimum legal size limits). Strategy 3 adds a 20% increase in YOY and early juvenile survival (e.g., by rehabilitating habitat and stocking YOY and juveniles). This is a conservative increase in these vital rates given their maximum proportional increases (73-100%). Strategy 4 maximizes the survival of late adults; this implies a total elimination of fishing mortality. Even though fertility rates make the smallest contributions to population growth rates, with maximum proportional increases ranging from 4-20%, Strategy 5 adds a 20% increase in fertility (e.g., through dam removal or passing spawners at barriers).

Maximizing the survival of young adults (Strategy 1) is predicted to produce recovery timeframes ranging from 50 years with an initial population vector (*IPV*) 10% of the recovery target (*ASF*) to 95 years with an *IPV* 1% of the recovery target (Figure 8). Increasing late juvenile survival 10% (Strategy 2) reduced recovery timeframes to 36 years when *IPV* = 0.1 *ASF* and 67 years when *IPV* = 0.01 *ASF*. Increasing YOY and early juvenile survival 20% (Strategy 3), is predicted to reduce recovery timeframes to 24 years when *IPV* = 0.1 *ASF* and 44 years when *IPV* = 0.01 *ASF*. Maximizing late adult survival (Strategy 4) further reduces recovery timeframes to 19 years when *IPV* = 0.1 *ASF* and 33 years when *IPV* = 0.01 *ASF*. Finally, increasing fertility 20%, had a small effect on recovery timeframes (18 years when *IPV* = 0.1 *ASF*; 33 years when *IPV* = 0.01 *ASF*; Figure 8).

The influence of spawning periodicity on recovery timeframes was inversely proportional to both the initial population vector and the proactive nature of the recovery strategy (Figure 9). Under Strategy 1, projections of recovery timeframes differed by 121 years when *IPV* = 0.01 *ASF* and 64 years when *IPV* = 0.1 *ASF*, or an average 329% variation across the *IPV* range. Under Strategy 2, projections of recovery timeframes differed by 49 years when *IPV* = 0.01 *ASF* and 31 years when *IPV* = 0.1 *ASF*; an average 234% variation. Projections of recovery timeframes for Strategy 3 differed by 28 years when *IPV* = 0.01 *ASF* and by 15 years when *IPV* = 0.1 *ASF*, indicating an average variation of 186%. Recovery timeframes

for Strategy 4 differed by 19 years when *IPV* = 0.01 *ASF* and 9 years when *IPV* = 0.1 *ASF*; an average variation of 163%. Finally, under Strategy 5, projections of recovery timeframes differed by 16 years when *IPV* = 0.01 *ASF* and 9 years when *IPV* = 0.1 *ASF*; an average variation of 158%.

DISCUSSION

Six main conclusions emerge from our analyses. First, even after assuming main causes of decline are removed following listing for endangered DUs 2 (Saskatchewan River), 4 (Red-Assiniboine River-Lake Winnipeg), and 5 (Winnipeg/English River) their geometric mean population growth rates still indicate declining populations. Second, maximum allowable harm among DUs 1 (Western Hudson Bay), 3 (Nelson River Mainstem), 6 (Lake of the Woods, Rainy River), and 7 (Southern Hudson Bay and James Bay), and the three sub-units of DU8 (Great Lakes-Western St. Lawrence) should not exceed reductions of 1.0-3.7% in adult survival, 1.8-8.2% in juvenile survival, 5.7-13.2% in YOY survival, and 7.1-49.3% in fertility rates. Further, maximum allowable harm should be most limited in DU1 and $DU8_C$ (St Lawrence system). Third, lake sturgeon population growth rates are most sensitive to changes in adult survival, particularly early adults, which can exhibit total lengths ranging from 89.5 to 154.0 cm and body weights ranging from 4.4 to 24.8 kg among DUs (Table 6). Fourth, minimum recovery efforts for individual vital rates necessary to reverse population declines in DUs 2, 4, and 5 were estimated at 6.0-28.7% increments in adult survival, 11.3-35.8% in juvenile survival, 29.6-39.7% in YOY survival, or 59.4-136.1% in fertility rates. Further, minimum recovery efforts should be greater in DU2 for early adult survival with a 6% increase or maximization of this vital rate to levels close to zero mortality, whichever is more feasible. High early adult survival may limit potential increases and therefore other vital rates might have to be improved simultaneously to achieve target population growth rates. Fifth, the stochastic-generic (i.e., parsimonious) model, with its greater variation in vital rates and transition probabilities, did not produce precautionary estimates of allowable harm and recovery efforts in all circumstances. Sixth, the uncertainty in recovery timeframes associated with spawning periodicity decreases with initial population size and with the proactive nature of the recovery strategy.

Our study demonstrates that changes in adult mortality have a large impact on lake sturgeon population fitness, consistent with the findings of Vélez-Espino et al. (2006) where lake sturgeon emerged as one of the few North American freshwater species where population growth rate is mostly sensitive to perturbations in adult survival. Similar patterns have been observed in shortnose sturgeon (*Acipenser brevirostrum*) and Atlantic sturgeon (*Acipenser oxyrinchus*) (Gross et al. 2002). Also consistent with the findings of Vélez-Espino et al. (2006), population growth rates of lake sturgeon are expected to be highly resilient to perturbations in fertility rates, particularly those of late adults ranging 112-165 cm of total length and 9-30 kg of body weight among all DUs (Table 6). Even though denial of access to spawning through dams and barriers is considered one of the most important causes of decline in sturgeons (e.g., Hay-Chmielewski and Whelan 1997, Dadswell 2006) since females either resorb their eggs (Artyukhin et al. 1978, Veshchev and Novikova 1988) or the survival of spawned eggs in suboptimal habitats is reduced (Auer 1996), maximum allowable harm on fertility rates of early adults and late adults can be 7-16 times and 18-49 times greater than in early adult survival, respectively. This has important implications for management because our analyses indicate that adult mortality (inflicted by fishing or other sources of mortality) is expected to have a substantially greater impact than relative impacts on reproduction. Nevertheless, continuous and

intense recruitment failure caused by blocking spawning migration by dams and barriers or habitat degradation can still produce more apparent population constraints than adult mortality (Jager et al. 2007).

Despite being able to obtain greater proportional increases in population growth rate by maximizing YOY and juvenile survival, recovery actions targeting increases in early adult survival are recommended because lower relative efforts will be needed to reach recovery targets. Nevertheless, an economic analysis of management options, using the information presented here on minimum recovery efforts should examine the possibility of implementing recovery strategies such as habitat rehabilitation to improve YOY and juvenile survival. The high feasibility indices of these vital rates support such an analysis. An integrated management strategy might attempt to target several vital rates simultaneously, in which case target population growth rates can be computed as:

10) $$\lambda_{Target} = \Lambda\left(1 + \sum_{v=1}^{n} \varepsilon_v \psi_v\right)$$

where n is the number of vital rates simultaneously improved and ψ_v is a recovery effort equal to or smaller than the maximum proportional increase in a vital rate.

Given that the stochastic-generic model was not the most conservative in several DUs, in spite of its incorporating greater uncertainty, managers might want to consider the use of the "most precautionary" values among all DUs as references for management decisions. More specifically, decisions involving allowable harm might take the precautionary values of DU1 and $DU8_C$ and decisions involving recovery efforts might consider the precautionary values of DU5 for YOY and juvenile survival, and the precautionary values of DU2 for adult survival. However, it would be necessary to consider that natural constraints to incrementing adult survival might limit recovery efforts for late adult survival.

Similarly, highly negative feasibility indices for fertility rates suggest that it would be extremely difficult to produce significant population improvements through management strategies to improve fertility rates. This does not mean that facilitating lake sturgeon passage around instream barriers and into spawning grounds should not be an important element of management strategies. Complete blockage of spawners at barriers can eradicate a population in a generation from continuous reproductive failure and strong site fidelity for spawning (Swanson et al. 1991, Rusak and Mosindy 1997, Barth and Ambrose 2006). In addition, there is evidence that hydroelectric facilities, for example, not only present an obstacle to lake sturgeon spawning migrations but constitute a source of adult mortality through entrainment and turbine mortality (Hay-Chmielewski and Whelan 1997). For such cases, with simultaneous perturbations of several vital rates (i.e., fertility and survival rates), a variant of equation 10 can be used to analyze population responses.

Commercial, recreational, and subsistence lake sturgeon harvest exists in most Canadian DUs but in few instances do fishing regulations include well defined minimum size limits or harvest size ranges (COSEWIC 2006). Regulations of lake sturgeon commercial harvest in Lake Huron ($DU8_A$) and recreational harvest in the St. Clair system in Michigan (the Canadian portion of the St. Clair System is part of $DU8_A$) include a minimum legal size limit of 109 cm total length in the former (Mohr 2000) and a harvest size range from 106.7 to 127.0 cm total length in the latter (Thomas and Haas 2002). A limited commercial harvest also exists for several reaches of the Ottawa River ($DU8_C$) with a minimum legal size limit of 83.3 cm total length (Haxton 2002). According to our estimates of total length for these

DU8 sub-units (Table 6), the above regulations would allow the capture of some immature individuals in these three systems as well as early and late adults from all sizes in Lake Huron and the Ottawa River. The harvest size range applied in the St. Clair system also allows the capture of large immature individuals but the capture of adults is limited to small early adults. The results of our analyses recommend that management of these populations should ensure that fishing mortality in individual stages does not exceed 3.7% in late juveniles, 2% in early adults, or 2.6% in late adults in $DU8_A$, and 1.8% in late juveniles, 1.1% in early adults, or 1.3% in late adults in $DU8_C$. However, fishing mortality on a composite stage (susceptible to fishing) including individuals from the late juvenile, early adult, and late adult stages would have to be limited to 0.9% for Lake Huron and 0.4% for the Ottawa River. Similarly, fishing mortality on a composite stage including late juveniles and early adults would have to be limited to 0.7% for the St. Clair system in Michigan. Although fishing mortality on these composite stages must be lower than for individual stages, it may represent higher numbers of fish depending on the structure of the population.

Stochastic projections of recovery timeframes indicated that a feasible management strategy, such as a total closure of the fishery for early adults, can result in recovery timeframes ranging from 50 to 95 years, depending on current population abundances. Recovery targets could be reached earlier (28-52 years) in lake sturgeon populations with greater reproductive effort and an average three year spawning periodicity. Conversely, recovery targets might not be attainable in less than 92-173 years in lake sturgeon populations exhibiting lower reproductive effort and an average seven year spawning periodicity. Further, by simultaneously reducing fishing mortality on late juveniles to effect a 10% increase in survival, recovery timeframes and the uncertainty associated with spawning periodicity are reduced substantially relative to a total closure of the fishery for early adults. Moreover, habitat rehabilitation and stocking of YOY and early juveniles can strongly reduce recovery timeframes. Modest increments in lake sturgeon passage at barriers and dams during upstream spawning migrations are expected to have a small role in an integrated recovery strategy.

Final remarks

Our demographic approach to the analysis of allowable harm and recovery effort using life history information provided new insights into the population dynamics of Canadian lake sturgeon populations that can guide future management decisions. Use of the precautionary approach is consistent with the level of variation in population responses and the uncertainty associated with our indirect estimates of vital rates. In spite of the important roles that latitude and longitude play in determination lake sturgeon growth, probably as a result of strong correlations with temperature and winter severity and duration (Power and McKinley 1997), there are additional factors not directly related to latitude or longitude such as pH, dissolved solids, conductivity, alkalinity, dissolved oxygen (e.g., Fortin et al. 1996) that could certainly influence growth at the local scale. In addition, there is evidence that variability in the diversity and abundance of macroinvertebrate communities, lake sturgeon prey, also influences growth and condition (Power and McKinley 1997, Jackson et al. 2002). For instance, our indirect estimate of asymptotic length for $DU8_C$ (173.7 cm) is higher than a recent estimate for the Ottawa River (133.7 cm; Haxton 2007), which is part of $DU8_C$. However, our indirect estimate of the growth coefficient for this DU sub-unit (k = 0.06) was representative of the growth coefficient (k = 0.058; 95% confidence interval: 0.052-0.064) recently estimated in the Ottawa River (Haxton 2007). However, note that DU1, which has an asymptotic length (126.8 cm)

similar to that of the Ottawa River, and $DU8_C$ exhibited the "most precautionary" values of allowable harm among all DUs, indicating that asymptotic length is not the main life history trait driving population responses to perturbations; rather, it is the combination of all vital rates and variances which determine population sensitivity to perturbations. Therefore, as a corollary to the above point, it seems appropriate to use the most precautionary values of allowable harm and recovery efforts in the presence of uncertainty associated with life history traits and corresponding vital rates.

The influences of density-dependence and covariation of vital rates on population responses of lake sturgeon at current abundances are elusive and remain a challenge to determining their contributions to demographic processes. Wide density-independent variation in vital rates was included in the stochastic approach, where the underlying assumption is not that density-dependence is absent but that the effect of density on population growth rate does not change over the range of population densities in the present and near future. A compensatory mechanism would increase population resilience to harm by assuming increased survival with decreased densities. Following a precautionary approach, the absence of density-dependence produces more risk-averse estimates than if we assumed compensation in spite of currently low densities. Moreover, vital rates do not vary independently; rather, they covary and important correlations can be ignored by the process of random variation when vital rates vary independently (Saether and Bakke 2000). Correlations among life history traits can have important impacts on population growth rates and are likely to alter the width of confidence intervals around population responses (e.g., Doak et al. 1994). The current state of knowledge about relationships among lake sturgeon life history traits precluded any attempt to incorporate vital rate covariation in our models. Our reliance on the precautionary approach is therefore consistent with this uncertainty and reverses the burden of proof when projected population responses are greater for recovery efforts and lower for allowable harm than actual responses (FAO 1996, Richards and Maguire 1998). Management plans should provide a buffer for uncertainties to safeguard the survival and recovery of imperiled populations. Ignoring type II errors (acceptance of the null hypothesis of no effect when in fact there is an impact) results in failure to recognize and avoid serious long-term damage such as the collapse of fisheries (Dayton 1998). The consequences of this type of error in the management of lake sturgeon populations can severely compromise their recovery potential given the low recovery rates exhibited by migratory, large, long-lived, late maturing organisms (Parent and Schrimi 1995).

Finally, a refined definition of recovery targets for individual lake sturgeon populations, providing more pragmatic recovery efforts and recovery timeframes, will require additional knowledge on the extent of habitat required to secure self-sustaining populations and achieve recovery goals (Vélez-Espino and Koops 2007*b*) and up-to-date knowledge on population size and structure. With information on the area required per spawner, the area required for spawning could be estimated and considered for management scenarios. So far, our study has identified the relative contributions of lake sturgeon vital rates to population responses to management throughout the Canadian range and theoretical probabilities of recovery and recovery timeframes based on population abundance and structure ascribed to extant populations. These are considered important steps towards the implementation of recovery strategies that are feasible and scientifically sound.

ACKNOWLEDGEMENTS

Special thanks to T.C. Pratt, W. Franzin, and T. Haxton for helping to compile lake sturgeon data and providing comments on earlier versions of this manuscript. This research was supported by funding from the DFO Species at Risk Program (SARCEP) and a Visiting Fellowship with the Great Lakes Laboratory for Fisheries and Aquatic Sciences to L.A. Vélez-Espino.

REFERENCES

Adams, W.E. 2004. Lake sturgeon biology in Rainy Lake, Minnesota and Ontario. M.Sc. Thesis. South Dakota State University. 92 p.

Auer, N.A. 1996. Importance of habitat and migration to sturgeons with emphasis on lake sturgeon. Can. J. Fish. Aquat. Sci. **53**(Suppl. 1): 152-160.

Baker, E.A., and Borgeson, D.J. 1999. Lake sturgeon abundance and harvest in Black Lake, Michigan, 1975-1999. N. Am. J. Fish. Manage. **19**: 1080-1088.

Barth, C.C., and Ambrose, K.M. 2006. Lake sturgeon investigations in the Keeyask study area, 2004. Keeyask Project Environmental Studies Program, Report 04-05. North/South Consultants Inc., Winnipeg, MB. 86 pp.

Beissinger, S.R., and McCullough, D.R. 2002. Population viability analysis. University of Chicago Press, Chicago.

Brault, S., and Caswell, H.. 1993. Pod-specific demography of killer whales (*Orcinus orca*). Ecology 74: 1444-1454.

Caswell, H. 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. Ecology 81: 619-627.

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts, USA.

Charnov, E.L. 1993. Life history invariants. Oxford University Press, Oxford, UK.

Cortés, E. 2002. Incorporating uncertainty into demographic modelling: application to shark populations and their conservation. Conservation biology **16**: 1048-1062.

COSEWIC. 2006. COSEWIC assessment and update status report on the lake sturgeon, *Acipenser fulvescens*, in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xi + 107 pp.

Crouse, D.T., Crowder, L.B., and Caswell, H. 1987. A stage-based population model for loggerhead turtles and implications for conservation. Ecology **68**: 1412-1423.

Dadswell, M.J. 2006. A review of the status of Atlantic sturgeon in Canada, with comparisons to populations in the United States and Europe. Fisheries **31:** 218-229.

Dayton, P.K. 1998. Reversal of the burden of proof in fisheries management. Science **279**: 821-822.

De Kroon, H., Plaiser, A., Groenendael, J.V., and Caswell, H. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. Ecology **67**: 1427-1431.

DFO. 2005a. Recovery assessment report for Interior Fraser coho salmon (*Oncorhynchus kisutch*). DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2005/061.

DFO. 2005b. Recovery potential assessment for winter skate on the Eastern Scotian Shelf (NAFO Division 4VW). DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2005/062.

DFO. 2005c. A framework for developing science advice on recovery targets for aquatic species in the context of the Species at risk Act. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2005/054.

Doak, D., Kareiva, P., and Klepetka, B. 1994. Modeling population viability for desert tortoise in the western Mojave Desert. Ecological Applications **4**: 446-460.

Earle, S. 2002. Status of the lake sturgeon (*Acipenser fulvescens*) in Alberta. Alberta Wildlife Status Report 46. Published by: Alberta Sustainable Resource Development, and Alberta Conservation Association. 40 p.

FAO. 1996. Precautionary approach to capture fisheries and species introductions. Rome: FAO, Technical Guidelines for Responsible Fisheries 2, 52 pp.

Fortin, R., Mongeau, J., Desjardins, G.,and Dumont, P. 1993. Movements and biological statistics of lake sturgeon (*Acipenser fulvescens*) populations from the St. Lawrence and Ottawa River system, Quebec. Canadian Journal of Zoology 71: 638-650.

Fortin, R., Dumont, P., and Guénette, S. 1996. Determinants of growth and body condition of lake sturgeon (*Acipenser fulvescens*). Can. J. Fish. Aquat. Sci. 53: 1150-1156.

Getz, W.M., and Haight, R.G. 1989. Population harvesting: demographic models of fish, forest, and animal resources. Monographs in Population Biology 27. Princeton University Press, Princeton, New Jersey, USA.

Gross, M.R., Repka, J., Robertson, C.T., Secor, D.H., and Van Winkle, W. 2002. Sturgeon conservation: insights from elasticity analysis. *In* Biology, management and protection of North American sturgeon. *Edited by* W. Van Winkle, P.J. Anders, D.H. Secor, and D.A. Dixon, editors. American Fisheries Society, Bethesda, Maryland. Pp.13-30

Hay-Chmielewski, E.M., and Whelan, G.E. 1997. Lake sturgeon rehabilitation. Fisheries Division Special Report, State of Michigan Department of Natural Resources, 51 p.

Hayes, D. 2000. A biological reference point based on the Leslie matrix. Fish. Bull. **98**: 75-85.

Haxton, T. 2002. An assessment of lake sturgeon (*Acipenser fulvescens*) in various reaches of the Ottawa River. J. Appl. Ichthyol. **18**: 119-454.

Haxton, T.J. 2007. Impacts of waterpower management on select fish in the Ottawa River, Canada, with an emphasis on lake sturgeon. Ph.D. Thesis. University of Ottawa, Ottawa, Canada.

Hitchcock, C.L., and Grato-Trevor, C.. 1997. Diagnosing a shorebird local population decline with a stage structured population model. Ecology **78**: 522-534.

Jackson, J.R., VanDeValk, A.J., Brooking, T.E.,. vanKeeken, O.A, and Rudstam, L.G.. 2002. Growth and feeding dynamics of lake sturgeon, *Acipenser fulvescens*, in Oneida Lake, New York: results from the first five years of a restoration program. J. Appl. Ichthyol. **18**: 439-443.

Jager, H.I., Bevelhimer, M.S., Lepla, K.B., Chandler, J.A, and Van Winkle, W. 2007. Evaluation of reconnection options for white sturgeon in the Snake River using a population viability model. American Fisheries society Symposium **56**: 319-335.

Jensen, A.L. 1996. Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. Can. J. Fish. Aquat. Sci. **53**: 820-822.

Koops, M.A., and Chu, C. 2007. The applicability of life history invariants in the Great Lakes. Great Lakes Fishery Commission Project Completion Report, Ann Arbor, MI.

MacDonnell, D.S. 1998. Lower Nelson River lake sturgeon spawning study Weir River 1997. A Report Prepared for Manitoba Hydro. North/South Consultants Inc., Winnipeg, MB. 63 pp.

Mertz, G., and Myers, R.A.. 1996. Influence of fecundity on recruitment variability of marine fish. Can. J. Fish. Aquat. Sci. **53**: 1618-1625.

Mills, L.S., Doak, D.F., and Wisdom, M.J. 1999. Reliability of conservation actions based on elasticity analysis of matrix models. Conservation Biol. **13**: 815-829.

Mohr, L. 2000. Lake sturgeon monitoring in Ontario waters of Lake Huron – 2000. Lake Huron Management Unit, Ontario Ministry of Natural Resources, Owen Sound, ON. 5 pp.

Morris, W.F., and Doak, D.F. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Sunderland, Massachusetts, USA.

Neubert, M.G., and Caswell, H. 2000. Demography and dispersal: invasion speeds of stage-structured populations. Ecology **81**: 1613-1628.

Parent, S., and Schrimi, L.M. 1995. A model for the determination of fish species at risk based upon life-history traits and ecological data. Can. J. Fish. Aquat. Sci. **52**: 1768-1781.

Peterson, D.L., Gunderman, B., and Vecsei, P. 2001. Lake Sturgeon of the Manistee River: A Current Assessment of Spawning Stock Size, Age, and Growth. Biology, Management, and Protection of North American Sturgeon. pp. 175-182. American Fisheries Society Symposium. Vol. 28.

Pianka, E.R. 1970. On *r*- and *K*-selection. Am. Nat. **104**: 592-597.

Power, M., and McKinley, R.S. 1997. Latitudinal variation in lake sturgeon size as related to the thermal opportunity to growth. Trans. Am. Fish. Soc. **126**: 549-558.

Randall, R.G., and Minns, C.K. 2000. Use of fish production per unit biomass ratios for measuring the productive capacity of fish habitats. Can. J. Fish. Aquat. Sci. **57**: 1657-1667.

Reed, D.H., O'Grady, J.J., Brook, B.W., Ballou, J.D., and Frankham, R. 2003. Estimates of minimum viable population sizes for vertebrates and factors influencing those estimates. Biol. Cons. **113**: 23-34.

Reznick, D., Bryant, M.J., and Bashey, F. 2002. *r*- and *K*-selection revisited: the role of population regulation in life history evolution. Ecology 83: 1509-1520.

Richards, L.J., and Maguire, J. 1998. Recent international agreements and the precautionary approach: new directions for fisheries management science. Can. J. Fish. Aquat. Sci. **55**: 1545-1552.

Rockwell, R., Cooch, E., and Brault, S. 1997. Dynamics of the mid-continent population of lesser snow geese: projected impacts of reductions in survival and fertility on population growth rates. *In* Artic ecosystems in peril: report of the Artic Goose Habitat Working Group. *Edited by* B.D.J. Batt. Artic Goose Joint Venture Special Publication. U.S. Wildlife Service, Washington D.C. and Canadian Wildlife Service, Ottawa, Ontario. pp. 71-97.

Rusak, J.A., and Mosindy, T. 1997. Seasonal movements of lake sturgeon in Lake of the Woods and the Rainy River, Ontario. Can. J. Zool. **74**: 383-395.

Saether, B.E., and Bakke, O. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology **81**: 642-653.

Sanderson, E.W. 2006. How many animals do we want to save? The many ways of setting population target levels for conservation. BioScience **56**: 911-922.

Scott, W.B., and Crossman, E.J. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. No. 184.

Scott, W.B., and Crossman, E.J. 1998. Freshwater fishes of Canada. Galt House Publications Ltd. Oakville, ON. 966 pp.

Shea, K., and Kelly, D. 1998. Estimating biocontrol agent impact with matrix models: *Carduus nutans* in New Zealand. Ecol. App. **8**: 824-832.

Sheffer, M.L. 1981. Minimum population sizes for species conservation. BioScience **31**: 131-134.

Stewart, K.W., and Watkinson, D.A.. 2004. The freshwater fishes of Manitoba. University of Manitoba Press, Winnipeg, MB. 276 pp.

Stewig, J.D. 2005. A population assessment of the lake sturgeon in Lake of the Woods and the Rainy River, 2004. Completion Report, Minnesota Department of Natural Resources, Fisheries Division. 38 p.

Swanson, G.M., Kansas, K.R., Matkowski, S.M., and Graveline, P. 1991. A report on the fisheries resource of the Lower Nelson River and the impacts of hydroelectric development, 1989 data. Manitoba Department of Natural Resources, Fisheries Branch, Manuscript Report 91-03. 248 pp.

Thomas, M.V., and. Haas, R.C. 2002. Abundance, age structure, and spatial distribution of lake sturgeon, *Acipenser fulvescens*, in the St. Clair System. J. Appl. Ichthyol. **18**: 495-501.

Turchin, P. 1995. Population regulation: old arguments and a new synthesis. *In* Population Dynamics. New approaches and Synthesis. *Edited by* N. Cappuccino and P.W. Price. Academic Press. Pp. 19-40.

U.S. Fish and Wildlife Service. 2006. Lake sturgeon biology. Great Lakes lake sturgeon website. www.fws.gov/midwest/sturgeon/biology.htm.

Vélez-Espino, L.A., Fox, M.G., and McLaughlin, R.L. 2006. Characterization of elasticity patterns of North American freshwater fishes. Can. J. Fish. Aquat. Sci. **63**: 2050-2066.

Vélez-Espino, L.A., and Koops, M.A.. 2007*a*. A quantitative approach to assessing allowable harm in species at risk: application to the Laurentian black redhorse (*Moxostoma duquesnei*). DFO Can. Sci. Advis. Sec. Res. Doc. 2007/051.

Vélez-Espino, L.A., and Koops, M.A. 2007*b*. Assessing allowable harm and recovery efforts in Lake Ontario Atlantic salmon (*Salmo salar*). DFO Can. Sci. Advis. Sec. Res. Doc. 2007/083.

Veshchev, P.V., and A.S. Novikova. 1988. Reproduction of sevryuga, *Acipenser stellatus*, in the lower Volga. J. Ichthyol. **28**: 3-47.

Wallace, R.G. 1991. Species recovery plan for lake sturgeon on the Lower Saskatchewan River (Cumberland House area). Fisheries Technical Report 91-3. Fisheries Branch, Saskatchewan Parks and Renewable Resources, Regina, SK. 51 pp.

Wilson, P.H. 2003. Using population projection matrices to evaluate recovery strategies for Snake River spring and summer salmon. Conservation Biol. **17**: 782-794.

Winemiller, K.O., and Rose, K.A. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. Can. J. Fish. Aquat. Sci. **49**: 2196-2218.

Table 1. Compiled life history traits of lake sturgeon (*Acipenser fulvescens*).

Trait	Mean	Min	Max	Other	Source
Adult survival	0.953				Adams 2004
Site fidelity for spawning				Strong	Barth and Ambrose 2006
Generation time (natural)		35	54		COSEWIC (2006)
Generation time in the present [a]		26	30		COSEWIC (2006)
Sex ratio (proportion of females) [b]	0.5				Fortin et al. 1993
Age at maturity		20	29		Fortin et al. 1993 (Quebec)
Survival for ages = 1 [c]		0.865	0.93		Gross et al. 2002
YOY survival [c,d]		0.0000007	0.00005		Gross et al. 2002
Survival	0.965				MacDonnell 1998
Site fidelity for spawning				Strong	Rusak and Mosindy 1997
Size at maturity (TL cm)		83.9	119.5		Scot and Crossman 1973
Age-length-weight relationship				Table	Scot and Crossman 1974
Asymptotic size (present) (kg)	40				Scott and Crossman 1998
Max. size (TL cm)			300		Stewart and Watkinson 2004
Max. weight (kg)			180		Stewart and Watkinson 2004
Max. reproductive age			150		Stewart and Watkinson 2004
Reproductive senescence				No evidence	Stewart and Watkinson 2004
Site fidelity for spawning				Strong	Swanson et al. 1991
Age at maturity	24	14	33		USFWS 2006
Eggs per kg of body weight	12000	9000	15000		USFWS 2006
Longevity			150		USFWS 2006
Adult survival	0.933	0.9175	0.9485		Velez-Espino et al. 2006
Early adult fertility (f4) [c]	103874	38508	169244		Velez-Espino et al. 2006
Late adult fertility (f5) [c]	236794	173602	300000		Velez-Espino et al. 2006
Early juvenile survival	0.2565				Velez-Espino et al. 2006
Late juvenile survival	0.6998				Velez-Espino et al. 2006
Asymptotic size (past) (cm)	300				Waddell 1970
Weight at maturity (kg)	13.6				Wallace 1991
Size at maturity (TL cm)			130		Wallace 1991
Spawning periodicity		3	7		Wallace 1991
Survival		0.816	0.962		Wallace 1991
Age at maturity	20				Winemiller and Rose 1992
Size at maturity (TL cm)	88.9				Winemiller and Rose 1992
Max. size (TL cm)	215.9				Winemiller and Rose 1992
Longevity	80				Winemiller and Rose 1992
Number of eggs (m)	385079		3000000		Winemiller and Rose 1992
Spawning periodicity	5				Winemiller and Rose 1992

a Generation time has been reduced drastically in the last decades. A generation time that is close to the age of first maturity indicates population stress (COSEWIC Status Report).

b Although sex ratio in adults is biased towards females, the proportion of eggs producing females (0.5) is the trait of interest in demographic modeling.

c Values corresponding to other North American sturgeon species (*Acipenser brevirostrum*, *A. oxyrinchus*, and *A. transmontanus*).

d Values estimated at equilibrium.

e Values estimated as the product of the number of eggs, sex ratio, and spawning periodicity. Computations used mean trait values provided by Winemiller and Rose (1992).

Table 2. Risk status, latitude (LAT) and longitude (LON) at the centroid (both in decimal format), total length (cm) at age 25 (TL_{25}), and von Bertalanffy asymptotic length (L_∞) and growth coefficient (k) for each Canadian lake sturgeon designatable unit (DU). DU8 (Great Lakes-St. Lawrence) was divided in three sub-units.

DU	Name	Status	LAT	LON	*TL*25	L_∞	*k*
1	Western Hudson Bay	Endangered	56.5	98.0	91.2	126.80	0.051
2	Saskatchewan River	Endangered	52.0	108.3	125.1	142.42	0.084
3	Nelson River Mainstem	Endangered	57.0	92.0	81.9	125.07	0.042
4	Red-Assiniboine River-Lake Winnipeg	Endangered	52.0	97.0	112.2	142.42	0.062
5	Winnipeg/English River	Endangered	50.0	95.5	120.3	149.36	0.065
6	Lake of the Woods, Rainy River	Special concern	48.5	94.0	125.9	154.57	0.067
7	Southern Hudson Bay and James Bay	Special concern	51.8	83.7	97.9	143.11	0.046
8A	Lake Erie-Lake Huron	Threatened	45.3	69.3	113.4	165.56	0.046
8B	North Lake Superior	Threatened	49.0	88.5	117.2	152.83	0.058
8C	St. Lawrence	Threatened	43.0	78.3	135.1	173.65	0.060

Table 3. Population growth rates in lake sturgeon designatable units (DUs) and subunits in DU8 (see text for detail). $\lambda_{designation}$: population growth rate determined by COSEWIC's criterion "A" for the status assessment of species based on observed or inferred rates of population decline ($\lambda_{designation} = 1$ was assigned to special concern populations; see text for details); λ_{max}: maximum population growth at low densities; Λ: geometric mean population growth rate used for the estimation of allowable harm and recovery efforts; λ_{Target}: target population growth rate computed as Λ^{-1} in DUs where Λ indicates declining-population (i.e., $\Lambda < 1$) scenarios. NA: not applicable.

DU	λ designation	λ max	Λ	λ Target
1	0.887	1.150	1.007	NA
2	0.887	1.103	0.993	1.007
3	0.887	1.173	1.013	NA
4	0.887	1.118	0.997	1.003
5	0.887	1.109	0.994	1.006
6	1.000	1.103	1.033	NA
7	1.000	1.139	1.044	NA
8A	0.933	1.117	1.014	NA
8B	0.933	1.112	1.012	NA
8C	0.933	1.095	1.007	NA

Table 4. Maximum allowable harm for annual survival (σ_j) and fertility (f_j) vital rates generated from three models applied to designatable units (DUs) and one generic model. Precautionary allowable harm ($\tau_{v,precautionary}$) is shown in bold. A **G** indicates that the generic approach (shown at the bottom of the table) produced the most precautionary value. Values smaller than -1 are shaded to highlight the impossibility of reducing a vital rate more than 100%; complete cancellation of these vital rates cannot bring population growth to equilibrium.

			Vital rate						
Model		**DU**	σ_1	σ_2	σ_3	σ_4	σ_5	f_4	f_5
Deterministic	(elasticities)	1	-0.096	-0.071	-0.033	-0.015	-0.046	-0.146	-0.276
Deterministic	(direct perturbation)	1	-0.096	-0.071	-0.033	-0.015	-0.046	-0.146	-0.276
Stochastic	(individual DUs)	1	**-0.061**	**-0.033**	**-0.018**	**-0.010**	**-0.013**	**-0.074**	**-0.237**
Deterministic	(elasticities)	3	-0.200	-0.147	-0.068	-0.026	-0.079	-0.306	-0.573
Deterministic	(direct perturbation)	3	-0.200	-0.147	-0.068	-0.026	-0.120	-0.306	-0.540
Stochastic	(individual DUs)	3	**-0.118**	**-0.066**	**-0.035**	**-0.017**	**-0.024**	**-0.142**	**-0.490**
Deterministic	(elasticities)	6	-0.316	-0.238	-0.120	-0.081	-0.301	-0.456	-0.860
Deterministic	(direct perturbation)	6	-0.290	-0.238	-0.130	-0.086	-0.301	-0.456	-0.860
Stochastic	(individual DUs)	6	-0.226	-0.137	-0.081	-0.051	-0.079	-0.275	-0.880
			G	**G**	**G**	**G**	**G**	**G**	**G**
Deterministic	(elasticities)	7	-0.520	-0.388	-0.188	-0.092	-0.333	-0.737	-1.0
Deterministic	(direct perturbation)	7	-0.450	-0.380	-0.210	-0.100	-0.333	-0.700	-1.0
Stochastic	(individual DUs)	7	-0.337	-0.200	-0.114	-0.062	-0.089	-0.393	-1.0
			G	**G**	**G**	**G**	**G**	**G**	**G**
Deterministic	(elasticities)	8A	-0.196	-0.146	-0.071	-0.028	-0.090	-0.296	-0.580
Deterministic	(direct perturbation)	8A	-0.196	-0.146	-0.071	-0.150	-0.030	-0.296	-0.500
Stochastic	(individual DUs)	8A	**-0.119**	**-0.066**	**-0.037**	**-0.020**	**-0.026**	**-0.143**	-0.498
									G
Deterministic	(elasticities)	8B	-0.143	-0.106	-0.051	-0.027	-0.085	-0.218	-0.413
Deterministic	(direct perturbation)	8B	-0.143	-0.106	-0.051	-0.130	-0.030	-0.218	-0.413
Stochastic	(individual DUs)	8B	**-0.096**	**-0.054**	**-0.031**	**-0.018**	**-0.025**	**-0.118**	**-0.363**
Deterministic	(elasticities)	8C	-0.083	-0.062	-0.030	-0.016	-0.049	-0.128	-0.235
Deterministic	(direct perturbation)	8C	-0.083	-0.062	-0.030	-0.066	-0.015	-0.128	-0.235
Stochastic	(individual DUs)	8C	**-0.057**	**-0.032**	**-0.018**	**-0.011**	**-0.013**	**-0.071**	**-0.205**
Stochastic	(generic)		-0.132	-0.082	-0.049	-0.029	-0.037	-0.159	-0.493

Table 4. Maximum allowable harm for annual survival (σ_i) and fertility (f_i) vital rates generated from three models applied to designatable units (DUs) and one generic model. Precautionary allowable harm ($\tau_{v,precautionary}$) is shown in bold. A **G** indicates that the generic approach (shown at the bottom of the table) produced the most precautionary value. Values smaller than -1 are shaded to highlight the impossibility of reducing a vital rate more than 100%; complete cancellation of these vital rates cannot bring population growth to equilibrium.

			Vital rate						
Model		**DU**	σ_1	σ_2	σ_3	σ_4	σ_5	f_4	f_5
Deterministic	(elasticities)	1	-0.096	-0.071	-0.033	-0.015	-0.046	-0.146	-0.276
Deterministic	(direct perturbation)	1	-0.096	-0.071	-0.033	-0.015	-0.046	-0.146	-0.276
Stochastic	(individual DUs)	1	**-0.061**	**-0.033**	**-0.018**	**-0.010**	**-0.013**	**-0.074**	**-0.237**
Deterministic	(elasticities)	3	-0.200	-0.147	-0.068	-0.026	-0.079	-0.306	-0.573
Deterministic	(direct perturbation)	3	-0.200	-0.147	-0.068	-0.026	-0.120	-0.306	-0.540
Stochastic	(individual DUs)	3	**-0.118**	**-0.066**	**-0.035**	**-0.017**	**-0.024**	**-0.142**	**-0.490**
Deterministic	(elasticities)	6	-0.316	-0.238	-0.120	-0.081	-0.301	-0.456	<-1.0
Deterministic	(direct perturbation)	6	-0.290	-0.238	-0.130	-0.086	<-1.0	-0.456	-0.860
Stochastic	(individual DUs)	6	-0.226	-0.137	-0.081	-0.051	-0.079	-0.275	-0.880
			G	**G**	**G**	**G**	**G**	**G**	**G**
Deterministic	(elasticities)	7	-0.520	-0.388	-0.188	-0.092	-0.333	-0.737	<-1.0
Deterministic	(direct perturbation)	7	-0.450	-0.380	-0.210	-0.100	<-1.0	-0.700	<-1.0
Stochastic	(individual DUs)	7	-0.337	-0.200	-0.114	-0.062	-0.089	-0.393	<-1.0
			G	**G**	**G**	**G**	**G**	**G**	**G**
Deterministic	(elasticities)	8A	-0.196	-0.146	-0.071	-0.028	-0.090	-0.296	-0.580
Deterministic	(direct perturbation)	8A	-0.196	-0.146	-0.071	-0.150	-0.030	-0.296	-0.500
Stochastic	(individual DUs)	8A	**-0.119**	**-0.066**	**-0.037**	**-0.020**	**-0.026**	**-0.143**	-0.498
									G
Deterministic	(elasticities)	8B	-0.143	-0.106	-0.051	-0.027	-0.085	-0.218	-0.413
Deterministic	(direct perturbation)	8B	-0.143	-0.106	-0.051	-0.130	-0.030	-0.218	-0.413
Stochastic	(individual DUs)	8B	**-0.096**	**-0.054**	**-0.031**	**-0.018**	**-0.025**	**-0.118**	**-0.363**
Deterministic	(elasticities)	8C	-0.083	-0.062	-0.030	-0.016	-0.049	-0.128	-0.235
Deterministic	(direct perturbation)	8C	-0.083	-0.062	-0.030	-0.066	-0.015	-0.128	-0.235
Stochastic	(individual DUs)	8C	**-0.057**	**-0.032**	**-0.018**	**-0.011**	**-0.013**	**-0.071**	**-0.205**
Stochastic	(generic)		-0.132	-0.082	-0.049	-0.029	-0.037	-0.159	-0.493

Table 5. Minimum recovery efforts for annual survival (σ_j) and fertility (f_j) vital rates generated from three models applied to designatable units (DUs) and one generic model. Precautionary recovery effort ($\psi_{v,precautionary}$) is shown in bold. A **G** indicates that the generic approach (shown at the bottom of the table) produced the most precautionary value. Maximum proportional increase in a vital rate, $(v_{j,max} - v_j) / v_j$, and biological feasibility for improvement in a vital rate, $\delta_j = ((v_{j,max} - v_j) / v_j) - \psi_{v,precautionary}$, are included in the table.

			Vital rate						
Model		**DU**	σ_1	σ_2	σ_3	σ_4	σ_5	f_4	f_5
Deterministic	(elasticities)	2	0.127	0.096	0.048	0.043	0.129	0.204	0.337
Deterministic	(direct perturbation)	2	0.129	0.095	0.046	0.041	0.105	0.204	0.355
Stochastic	(individual DUs)	2	0.249	0.232	0.103	**0.060**	**0.287**	0.661	0.438
			G	**G**	**G**			**G**	**G**
	$(v_{j,max} - v_j) / v_j$	2	1.000	0.733	0.263	0.161	0.161	0.088	0.041
	δ_j	2	0.704	0.460	0.150	0.101	-0.126	-0.831	-0.553
Deterministic	(elasticities)	4	0.069	0.051	0.024	0.014	0.040	0.109	0.188
Deterministic	(direct perturbation)	4	0.078	0.056	0.026	0.015	0.038	0.120	0.210
Stochastic	(individual DUs)	4	0.214	0.194	0.109	0.023	0.115	0.718	0.365
			G	**G**	**G**	**G**	**G**	**G**	**G**
	$(v_{j,max} - v_j) / v_j$	4	1.000	0.733	0.263	0.114	0.114	0.204	0.077
	δ_j	4	0.704	0.460	0.150	0.071	-0.158	-0.715	-0.517
Deterministic	(elasticities)	5	0.135	0.100	0.048	0.028	0.083	0.214	0.366
Deterministic	(direct perturbation)	5	0.138	0.100	0.046	0.027	0.067	0.214	0.390
Stochastic	(individual DUs)	5	**0.397**	**0.358**	**0.182**	**0.047**	0.242	**1.361**	**0.624**
							G		
	$(v_{j,max} - v_j) / v_j$	5	1.000	0.733	0.263	0.120	0.120	0.183	0.072
	δ_j	5	0.603	0.375	0.081	0.073	-0.152	-1.178	-0.552
Stochastic	(generic)		0.296	0.273	0.113	0.043	0.272	0.919	0.594

Table 6. Maximum reproductive age (MRA) computed as age at 95% of asymptotic length, and length and weight ranges for early and late adult lake sturgeon (*Acipenser fulvescens*) in Canadian designatable units (DU).

		Early adult		Late adult	
DU	**MRA**	**Length range**	**Weight range**	**Length range**	**Weight range**
1	59	89.5 - 111.9	4.4 - 8.9	112.0 - 120.5	9.0 - 11.2
2	36	123.5 - 131.0	12.1 - 14.6	131.1 - 135.5	14.7 - 16.3
3	71	79.4 - 108.4	3.0 - 8.0	108.5 - 118.7	8.1 - 10.7
4	48	110.3 - 127.1	8.5 - 13.3	127.2 - 135.2	13.4 - 16.1
5	46	118.0 - 134.0	10.5 - 15.7	134.1 - 141.8	15.8 - 18.8
6	45	123.6 - 139.8	12.2 - 17.9	139.9 - 147.0	18.0 - 21.0
7	65	95.7 - 125.1	5.4 - 12.6	125.2 - 135.9	12.7 - 16.4
8A	65	110.7 - 144.7	8.6 - 20.0	144.8 - 157.2	20.1 - 26.0
8B	52	114.8 - 136.0	9.7 - 16.5	136.1 - 145.3	16.6 - 20.3
8C	50	132.5 - 154.8	15.2 - 24.8	154.9 - 165.0	24.9 - 30.3

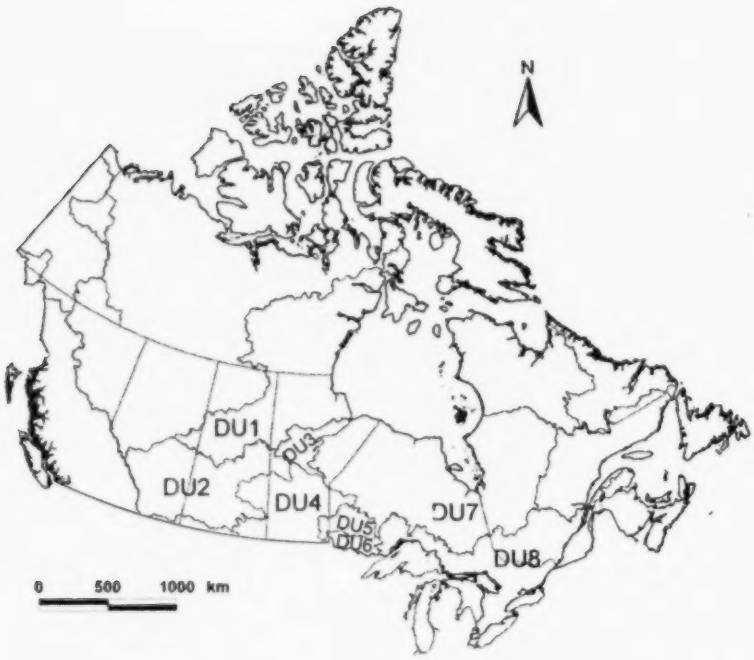


Figure 1. Lake sturgeon designatable units (DUs). Dark lines represent divisions between ecozones used by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). Light lines represent subdivision of ecozones into further designatable units based on available genetic information. DU1 – Western Hudson Bay; DU2 – Saskatchewan River; DU3 – Nelson River Mainstem; DU4 – Red-Assinibine River – Lake Winnipeg; DU5 – Winnipeg/English Rivers; DU6 – Lake of the woods - Rainy River; DU7 – Southern Hudson Bay and James Bay; DU8 – Great Lakes-Western (Upper) St. Lawrence.

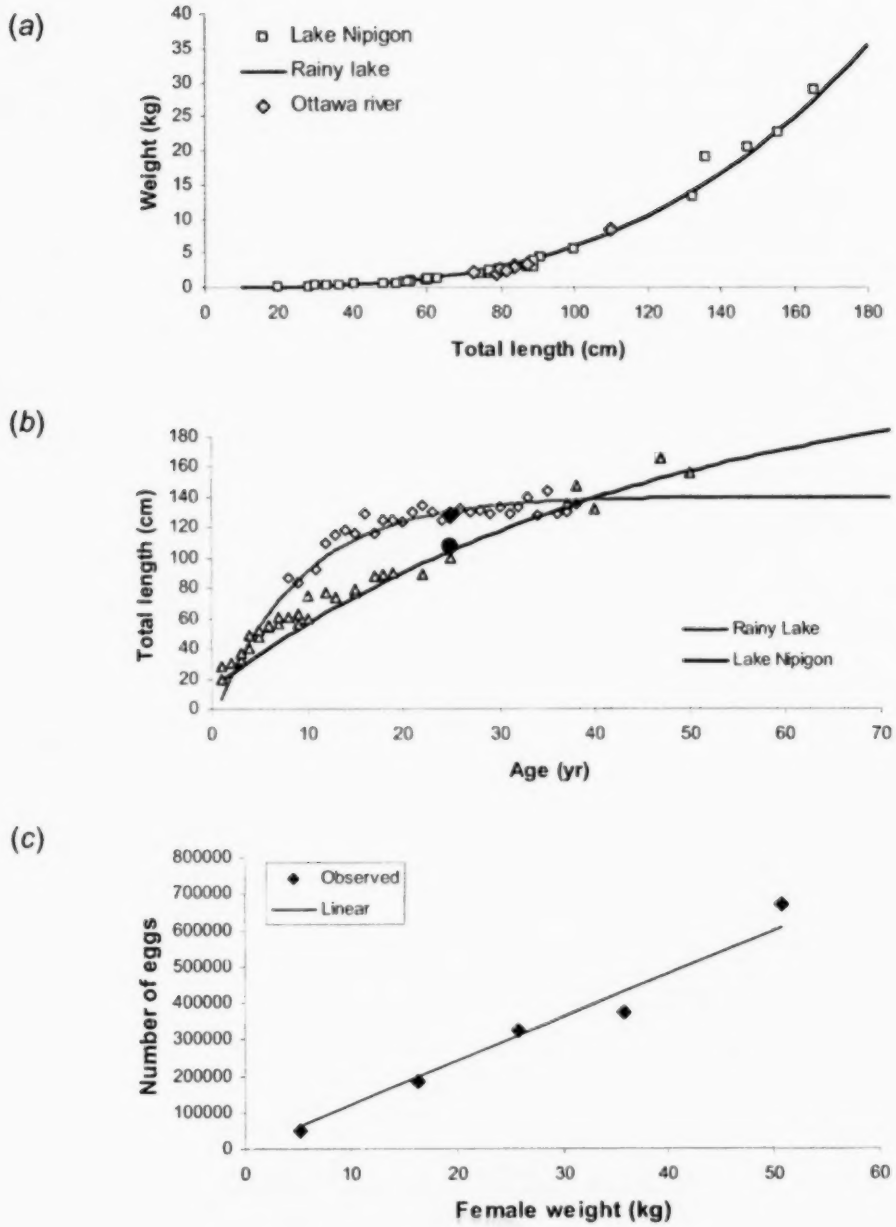
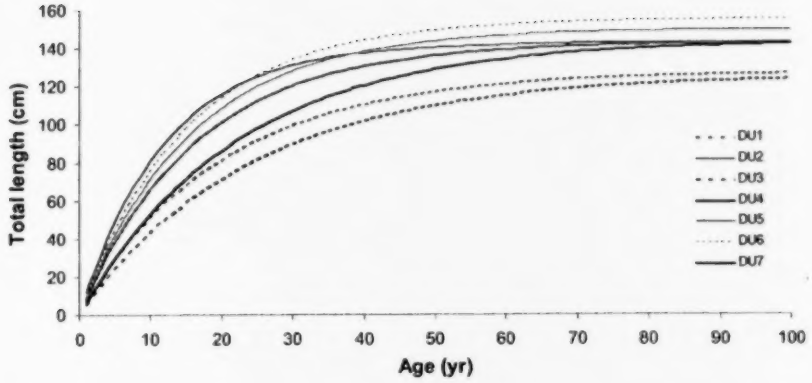
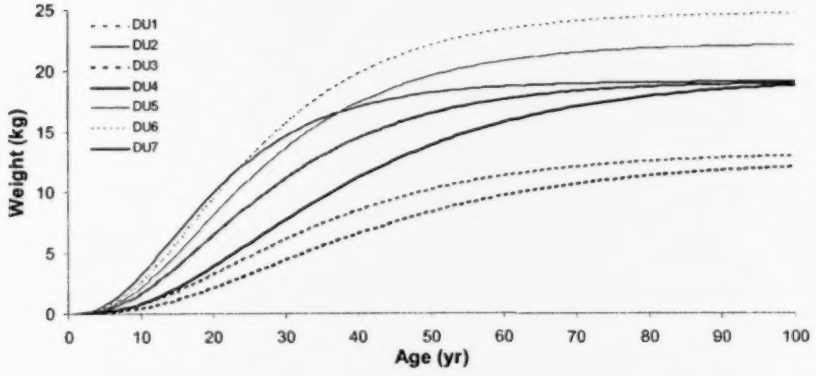


Figure 2. Growth and fertility patterns observed in some lake sturgeon populations. (*a*) Length and weight relationship for three lake sturgeon populations: Lake Nipigon (Scott and Crossman 1973), Ottawa River (Haxton 2002), Rainy Lake (Adams 2004); (*b*) Growth patterns of two lake sturgeon populations. Solid lines from von Bertalanffy model. Rainy Lake (diamonds): L_t (cm) = 140.38 (1-exp $^{-0.11(t - 0.56)}$); Lake Nipigon (triangles): L_t (cm) = 229.8 (1-exp $^{-0.02(t +2.8)}$). Large symbols represent predicted size at age 25 using Fortin et al.'s (1996) equation: Circle represents Lake Nipigon; Diamond represents Rainy Lake; (*c*) Female lake sturgeon weight-fecundity relationship. Observed data (Scott and Crossman 1973); linear relationship represents 12 000 eggs per kg body weight (USFWS 2006).

(a)



(b)



(c)

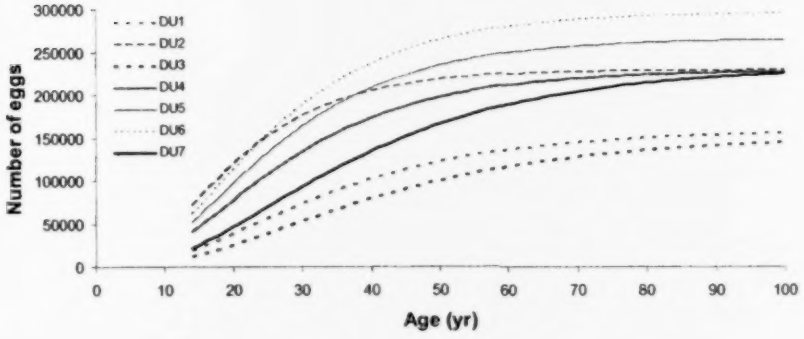


Figure 3. Growth and fecundity for seven lake sturgeon designatable units (DU's). DU1 – DU7 as identified in Table 2 and Figure 1. (*a*) Length at age. (*b*) Weight at age. (*c*) Number of eggs at age.

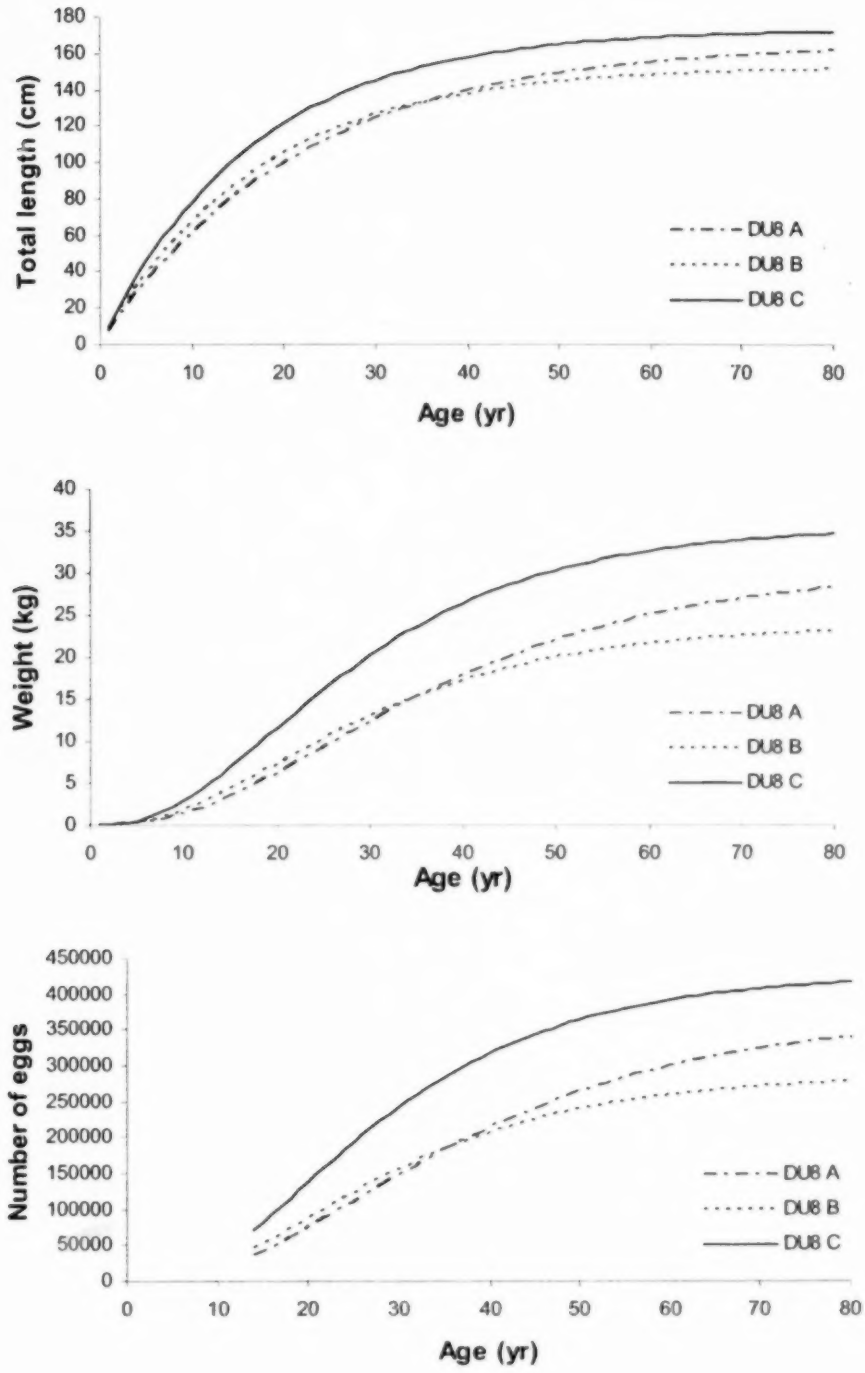
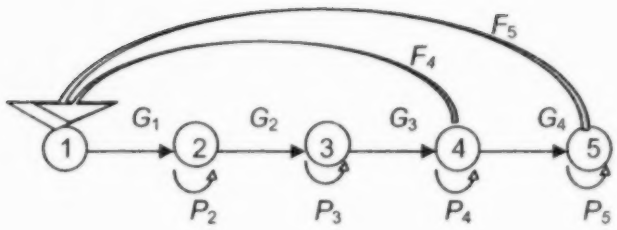


Figure 4. Growth and fecundity for three subunits within lake sturgeon designatable unit 8 (DU8), Great Lakes-Western St. Lawrence, as identified in Table 2 and Figure 1. (*a*) Length at age. (*b*) Weight at age. (*c*) Number of eggs at age.

a)



b)

$$\mathbf{A} = \begin{pmatrix} 0 & 0 & 0 & F_4 & F_5 \\ G_1 & P_2 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 & 0 \\ 0 & 0 & G_3 & P_4 & 0 \\ 0 & 0 & 0 & G_4 & P_5 \end{pmatrix}$$

c)

$$\mathbf{A} = \begin{pmatrix} 0 & 0 & f_4 G_3 & f_4 P_4 + f_5 G_4 & f_5 P_5 \\ \sigma_1 \gamma_1 & \sigma_2 (1-\gamma_2) & 0 & 0 & 0 \\ 0 & \sigma_2 \gamma_2 & \sigma_3 (1-\gamma_3) & 0 & 0 \\ 0 & 0 & \sigma_3 \gamma_3 & \sigma_4 (1-\gamma_4) & 0 \\ 0 & 0 & 0 & \sigma_4 \gamma_4 & \sigma_5 (1-\gamma_5) \end{pmatrix}$$

Figure 5. Generalized life cycle (a), corresponding stage-structured projection matrix (b), and matrix including formulas applied to calculate corresponding matrix elements (c) used to model the population dynamics of lake sturgeon. The life cycle was dived into five stages; young-of-the-year, small juveniles, large juveniles, young adults and old adults, respectively. F_j represents the stage-specific fecundity coefficient, P_j the probability of surviving and remaining in the same stage, and G_j the probability of surviving and moving to the next stage. The annual survival in stage j is σ_j, and the probability of growth from j to j+1 given σ_j is γ_j.

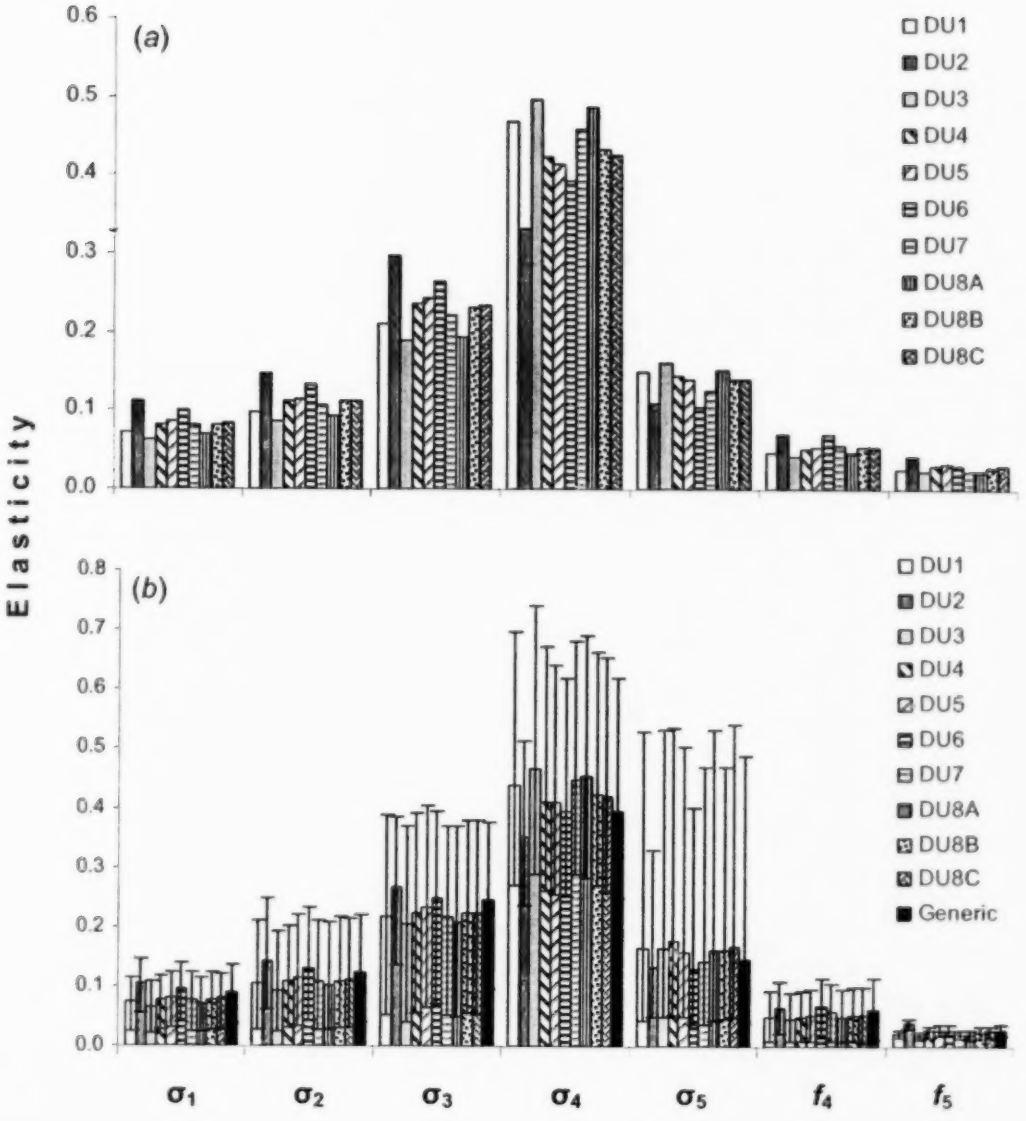


Figure 6. Vital rate elasticities of lake sturgeon designatable units (DUs). (*a*) Elasticities computed from mean matrices; (*b*) Elasticities computed from random matrices. An additional column represents the elasticity values computed from the generic approach (see text for details). Bars indicate 95% confidence intervals. σ_j is the annual survival rate in stage *j*. f_j is the fertility of stage *j*.

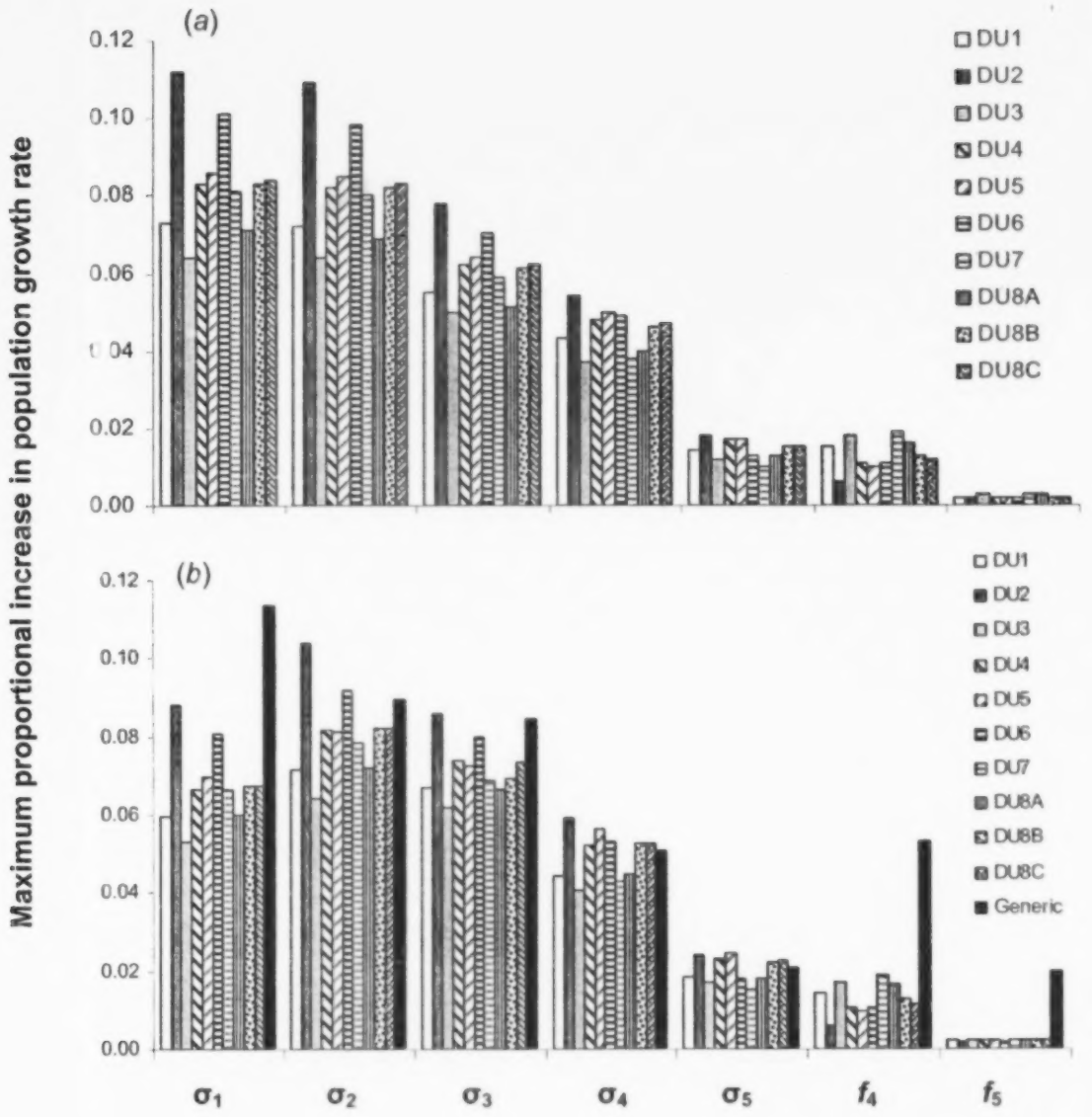


Figure 7. Maximum proportional increases in population growth ($\Delta\lambda/\lambda$). (*a*) Computed with deterministic elasticities; (*b*) Computed with stochastic elasticities. An additional column represents the elasticity values computed from the generic approach (see text for details). σ_j is the annual survival rate in stage j. f_j represents the fertility of stage j.

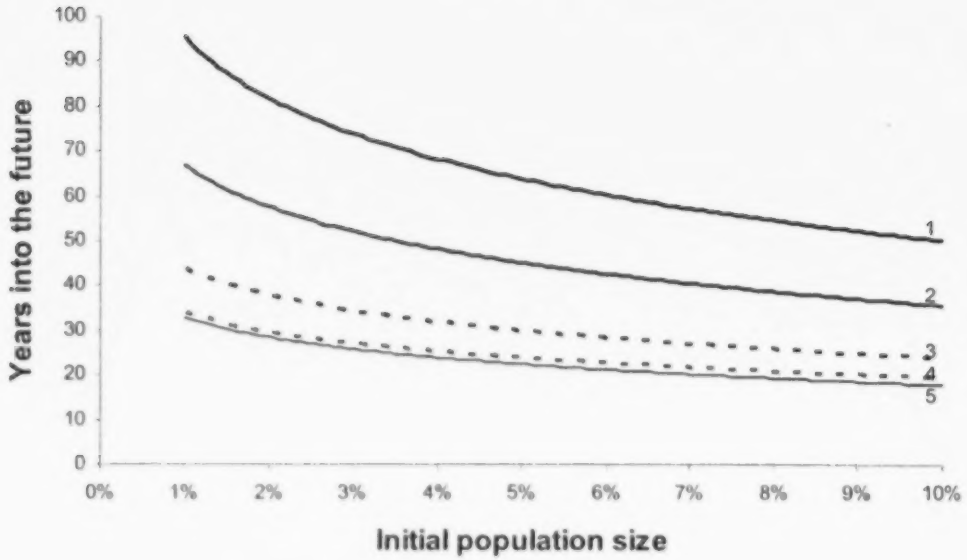


Figure 8. Stochastic projections of recovery timeframes under five different recovery strategies (see text for details). Initial population size is expressed as a percentage of the recovery target.

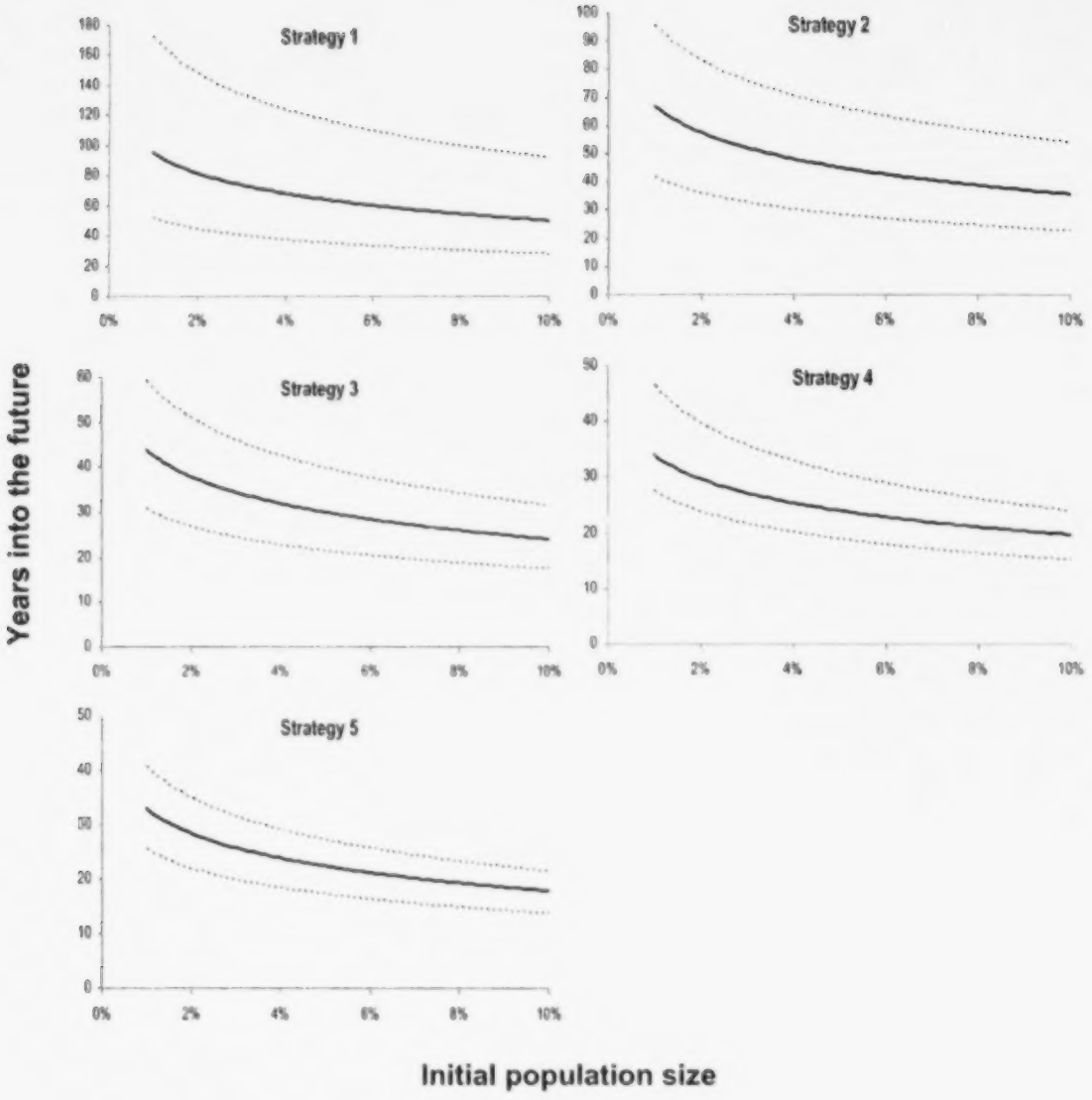


Figure 9. Sensitivity of stochastic projections of recovery timeframes to spawning periodicity for five different recovery strategies (see text for details). Solid line: average spawning periodicity of five years. Dashed lines: average spawning periodicity of three (lower line) and seven (higher line) years.

APPENDIX

Mean, variance, minimum, and maximum vital rates for lake sturgeon designatable units (DU) and a generic population. σ_j is annual survival rate in stage j. f_j is fertility of stage j.

		Vital rate						
	DU	σ_1	σ_2	σ_3	σ_4	σ_5	f_4	f_5
Mean	1	0.00187	0.29	0.73	0.92	0.92	8 159	12 332
Variance			0.02	0.02			2 888 871	672 501
Minimum		0.00094			0.87	0.87		
Maximum		0.00374	0.50	0.92	1.00	1.00	10 673	13 496
Mean	2	0.00213	0.27	0.68	0.86	0.86	16 122	18 767
Variance			0.02	0.01			1 156 174	357 920
Minimum		0.00107			0.82	0.82		
Maximum		0.00426	0.47	0.86	1.00	1.00	17 536	19 528
Mean	3	0.00183	0.29	0.74	0.93	0.93	6 802	11 533
Variance			0.02	0.02			3 512 495	864 709
Minimum		0.00092			0.88	0.88		
Maximum		0.00366	0.50	0.93	1.00	1.00	9 654	12 865
Mean	4	0.00142	0.28	0.71	0.90	0.90	13 268	17 984
Variance			0.02	0.02			3 545 628	991 182
Minimum		0.00071			0.85	0.85		
Maximum		0.00284	0.49	0.90	1.00	1.00	15 969	19 373
Mean	5	0.00126	0.28	0.71	0.89	0.89	15 940	21 061
Variance			0.02	0.02			4 213 647	1 182 828
Minimum		0.00063			0.85	0.85		
Maximum		0.00252	0.48	0.89	1.00	1.00	18 857	22 568
Mean	6	0.00173	0.28	0.70	0.89	0.89	18 656	23 750
Variance			0.02	0.02			5 167 914	1 196 427
Minimum		0.00087			0.84	0.84		
Maximum		0.00346	0.48	0.89	1.00	1.00	21 532	25 254
Mean	7	0.00188	0.29	0.73	0.92	0.92	11 320	17 829
Variance			0.02	0.02			7 290 543	1 748 825
Minimum		0.00094			0.88	0.88		
Maximum		0.00376	0.50	0.92	1.00	1.00	15 156	19 717
Mean	8A	0.0009	0.29	0.73	0.92	0.92	17 936	28 250
Variance			0.02	0.02			18 305 093	4 390 949
Minimum		0.00045			0.88	0.88		
Maximum		0.0018	0.50	0.92	1.00	1.00	24 016	31 243
Mean	8B	0.00126	0.28	0.72	0.90	0.90	15 943	22 475
Variance			0.02	0.02			6 847 143	1 818 418
Minimum		0.00063			0.86	0.86		
Maximum		0.00252	0.49	0.90	1.00	1.00	19 740	24 370
Mean	8C	0.00082	0.28	0.71	0.90	0.90	24 361	33 667
Variance			0.02	0.02			13 871 849	3 765 990
Minimum		0.00041			0.86	0.86		
Maximum		0.00164	0.49	0.90	1.00	1.00	29 735	36 385
Mean	Generic	0.00151	0.28	0.72	0.90	0.90	14 851	20 765
Variance			0.02	0.01			33 616 761	48 791 814
Minimum		0.00041			0.82	0.82		
Maximum		0.00426	0.50	0.93	1.00	1.00	29 735	36 385